OPERATIONALIZING THE CONCEPTS OF RESILIENCE AND RESISTANCE FOR MANAGING ECOSYSTEMS AND SPECIES AT RISK

EDITED BY: Jeanne C. Chambers, Craig R. Allen and Samuel A. Cushman

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frontiers Research Topics

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OPERATIONALIZING THE CONCEPTS OF RESILIENCE AND RESISTANCE FOR MANAGING ECOSYSTEMS AND SPECIES AT RISK

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EDITORIAL
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Editorial: Operationalizing the Concepts of Resilience and Resistance for Managing Ecosystems and Species at Risk

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Editorial on the Research Topic

Operationalizing the Concepts of Resilience and Resistance for Managing Ecosystems and Species at Risk

Ecological resilience is essential for maintaining ecosystem services in an era of rapid global change, but successful attempts to operationalize it for managing ecosystems at risk have been limited. Clear formulation and application of ecological resilience concepts can guide ecosystem management so that it enhances the capacity of ecosystems to resist and recover from disturbances and provides adaptive space for periods of ecological reorganization. As originally defined, ecological resilience measures the amount of perturbation required to change an ecosystem from one set of processes and structures to a different set of processes and structures, or the amount of disturbance that a system can withstand before it shifts into a new regime or alternative stable state (Holling, 1973). In applied ecology, ecological resilience is increasingly used to evaluate the capacity of ecosystems to absorb, persist, and adapt to inevitable and often unpredictable change, and to use that information to determine the most effective management strategies (e.g., Chambers et al., 2014; Curtin and Parker, 2014; Pope et al., 2014; Seidl et al., 2016).

As the scale and magnitude of ecological change increases, operationalizing ecological resilience for ecosystem management becomes ever more important. To date, much of the literature on ecological resilience has focused on theory, definitions, and broad conceptualizations (e.g., Gunderson, 2000; Folke et al., 2004, 2010; Walker et al., 2004; Folke, 2006; Gunderson et al., 2010). Much of the more applied research has focused on the importance of species diversity and species functional attributes in affecting responses to stress and disturbance (e.g., Pope et al., 2014; Angeler and Allen, 2016; Baho et al., 2017; Roberts et al., 2018).

Recent, interdisciplinary research demonstrates that information on the relationships between an ecosystem's environmental characteristics (climate, topography, soils, and potential biota) and its response to stress and disturbance provides a viable mechanism for assessing ecosystem resilience and relative risks (Chambers et al., 2014; Hessburg et al., 2016; Cushman et al., 2017; Kaszta et al., 2019). Approaches have been developed that enable application of resilience concepts at the scales needed for effective management of ecosystems experiencing progressive and deleterious change. For example, in the sagebrush biome of the western U.S. the concepts of resilience to fire and resistance to non-native invasive annual grasses have recently been used in an interagency framework to enhance conservation and restoration and help prevent listing of greater

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sage-grouse (*Centrocercus urophasianus*) under the Endangered Species Act (Chambers et al., 2017). In ecosystems around the globe, levels of ecological stress and disturbance are increasing while resources for natural resources management remain limited. Fully developing the capacity to operationalize the concept of ecological resilience can enable managers to prioritize the types and locations of management activities needed to optimize ecosystem conservation and restoration.

This Research Topic includes a series of articles that address key questions for operationalizing ecological resilience and describes applications of ecological resilience concepts and approaches in natural resources management. Examples are included from a variety of ecosystem types and spatial and temporal scales.

WHAT IS THE BASIS FOR APPLYING THE CONCEPT OF ECOSYSTEM RESILIENCE TO CONSERVATION AND RESTORATION MANAGEMENT?

A resilience-based approach to management can facilitate regional planning by guiding the allocation of management resources to where they will have optimal socioecological benefits. This type of approach requires a sound understanding of the environmental factors, ecosystem attributes and processes, and landscape components that influence ecological resilience of the focal system. Chambers et al. review and integrate resilience concepts to help inform natural resources management decisions for ecosystems and landscapes. They describe the six key components of a resilience-based approach, beginning with managing for adaptive capacity and selecting an appropriate spatial extent and grain. Additional components include developing an understanding of the factors influencing the general and ecological resilience of ecosystems and landscapes, the landscape context and spatial resilience, pattern and process interactions and their variability, and relationships among ecological and spatial resilience and the capacity to support habitats and species. They suggest that a spatially explicit approach that couples geospatial information on general and spatial resilience to disturbance with information on resources, habitats, or species provides the foundation for resilience-based management. A case study from the sagebrush biome is provided that is widely used by the management agencies.

HOW CAN RESILIENCE TO DISTURBANCE BE EVALUATED AND QUANTIFIED AT THE SCALES NEED TO FULLY OPERATIONALIZE THE CONCEPT?

Developing an understanding of ecological resilience and operationalizing resilience-based management has become more tractable with the rapid increase in models and decision-support tools from the field of landscape ecology. Cushman and McGarigal present metrics and describe a process for using geospatial data, landscape pattern analysis, and spatially dynamic simulation modeling to evaluate ecological resilience at scales relevant for management. The dynamic equilibria of species abundances, community structure, and landscape patterns that are produced under a given combination of abiotic conditions, such as topography, soils, and climate, can form a foundation to define desired conditions and measure resistance and resilience. The degree of forcing required to push a system from this dynamic range is a measure of resistance, and the rate of return to the dynamic range after the perturbation is a measure of the resilience and recovery of the system. The authors describe tools that are useful in defining the dynamic range of an ecosystem under natural regulation and measuring the forcing required to drive departure and the rate of recovery, including simulation models, landscape pattern analyses, and multivariate trajectory analysis.

Uden et al. provide a new approach that uses spatial imaging-based screening to detect ecological regime shifts (i.e., vegetation state transitions) that are known to be detrimental to human well-being and ecosystem service delivery. They use a landcover dataset and a freely available, cloud-based, geospatial computing platform to screen for spatial signals of three common vegetation transitions in western USA rangelands: (1) erosion and desertification; (2) woody encroachment; and (3) annual non-native grass invasion. A series of locations that differ in ecological complexity and geographic extent are used to ask: (1) Which regime shift is expected or of greatest concern? (2) Can we detect a signal associated with the expected regime shift? (3) If detected, is the signal transient or persistent over time? (4) If detected and persistent, is the transition signal stationary or non-stationary over time? (5) What other signals do we detect? The approach enables managers to use spatial imaging to verify the occurrence of alternative vegetation regimes and track the type and magnitude of regime shift signals for more targeted evaluation (e.g., inventory and monitoring) and treatment of regime shifts.

Assessing landscape patterns in ecological resilience to climate vulnerability, disturbance and invasive species requires appropriate metrics of relevant environmental conditions. In dryland systems of western North America, soil temperature and moisture regimes identified in the National Soil Survey provide integrative indicators of long-term site aridity and have been widely used to evaluate resilience to disturbance and resistance to non-native invasive plant species. Bradford et al. used a process-based, ecosystem water balance model to characterize current and future patterns in soil temperature and moisture conditions in these drylands and evaluate the impact of changes in these conditions on estimation of resilience and resistance. Results indicate widespread geographic shifts in the distribution of soil temperature and moisture regimes, but inconsistencies in the direction of change for certain regimes. The use of ecologically relevant soil water balance metrics as indicators of ecological resilience and resistance may enhance the ability to project change as the climate warms.

Model study systems and organisms can be used to increase our understanding of patterns and processes of various aspects of regime dynamics at tractable time scales. Angeler et al. posit that ecological systems can manifest in and change between

alternative regimes. They used discontinuity analysis to assess resilience attributes of spring and summer phytoplankton blooms based on a cross-scale resilience model and demonstrated that phytoplankton can be suitable models for assessing the intricacies of regimes and regime changes.

HOW HAVE RESILIENCE CONCEPTS BEEN USED TO INFORM ECOSYSTEM CONSERVATION AND RESTORATION AT OPERATIONAL SCALES?

Understanding ecosystem properties that reinforce ecological resilience and resistance in managed ecosystems can provide the basis for helping landscapes, species, and human communities adapt to changing conditions while maintaining core ecosystem processes and services. Hessburg et al. review the historical properties of western North American forests that reinforced resilience and resistance and show how multi-level landscape resilience, feedbacks within and among levels, and ecological conditions have changed under climatic and management influences. They discuss forest resilience and resistance to disturbances and the role of changes in regional climate and fire regimes in episodically reorganizing both plant and animal biogeography. They suggest that managing for resilient forests strongly depends on scale and human social values and requires embracing ongoing disturbances, anticipating effects of climatic changes, and supporting shifting patchworks of forest and non-forest.

Chambers et al. present new, spatially explicit approaches and decision-support tools that enable managers to better understand resilience to fire and resistance to non-native invasive annual grasses in dryland ecosystems and make more informed decisions. They review the abiotic and biotic factors that influence fire regimes, resilience to fire, resistance to non-native invasive annual grasses, and thus invasive grass-fire cycles, in global arid and semi-arid shrublands and woodlands. The Cold Deserts, Mediterranean Ecoregion, and Warm Deserts of North America are used as model systems to describe how and why resilience to disturbance and resistance to non-native invasive annuals differ over large landscapes. The Cold Deserts are used to illustrate an approach and decision-support tools for prioritizing areas on the landscape for management actions to prevent development of invasive grass-fire cycles and protect high value resources and habitats.

Ricca and Coates suggest that higher trophic-level fauna need to be included in tools to operationalize ecological resilience concepts because of spatiotemporal lags between slower reorganization of plant and soil processes and faster behavioral and demographic responses of fauna following disturbances. They provide multi-scale examples of decision-support tools for management and restoration actions in sagebrush ecosystems that evaluate ecological resilience based on variation in soil climate regimes through new lenses of habitat selection and population performance responses of an at-risk obligate species, the greater sage-grouse (*Centrocercus urophasianus*). They propose a targeted, operational approach to manage resilience that uses quantifiable metrics to limit spatiotemporal mismatches in restoration actions due to differences in sagebrush ecosystem recovery processes and sage-grouse population dynamics and identifies both active and passive management treatments across space and time.

HOW CAN ECOLOGICAL RESILIENCE APPROACHES BE USED TO HELP ECOSYSTEMS AND THE COMMUNITIES THAT DEPEND ON THEM ADAPT TO INEVITABLE CHANGE?

Management approaches based on ecological resilience can help communities prepare for, absorb, and adapt to change, but to be effective they must address the socioecological complexity of human-ecosystem interactions. Law can play an important role in promoting the resilience of ecosystems and communities to environmental change. Garmestani et al. suggest that as the climate warms and sea level rises, most coastal nations will need to transition to approaches based on ecological resilience and the law will be critical in facilitating this transition. They compare laws governing coastal zone management in Australia, Finland, and the Netherlands, and demonstrate that countries can adopt coastal zone management techniques that integrate social-ecological resilience. Importantly, they suggest that law-and-resilience research is needed to identify critical variables or sets of variables associated with countries' decisions to adopt laws designed to promote social-ecological resilience and mechanisms that allow for a smoother transition to this approach.

Using resilience concepts to characterize systems, and the social and ecological processes affecting them, is a way to integrate resilience into better management decisions. However, assessments of resilience are often challenging in complex socioecological systems facing unpredictable and unavoidable change. Lam et al. synthesize progress on the measurement of resilience on coral reefs and identify several novel, additional concepts that may have utility. Seven broad approaches are described under the three principle concepts of (1) ecological resilience (ecological resilience, precariousness and current attractor), (2) engineering resilience (short-term recovery rate and long-term reef performance), and (3) vulnerability (absolute and relative vulnerability, respectively). They evaluate both the strengths and limitations of each approach and their capacity to answer common management questions.

Camp et al. propose a framework based on inland recreational fisheries that allows resilience concepts to be better incorporated into management. The components are (1) recognizing how constraints and management objectives focus on desired or undesired systems; (2) evaluating how both social and ecological forces enforce or erode the desired or undesired system state; (3) identifying the resilience-stage cycles a system state may undergo; and (4) determining broad management strategies given the system state and resilience stage. They evaluate different system state and resilience stages and derive five management strategies: (1) adopt a different management preference or focus; (2) change stakeholder attitudes or behaviors

via stakeholder outreach; (3) engage in biological intervention; (4) engage in fishery intervention; and (5) adopt landscape management approaches focusing on achieving different systems in different waters.

Kurth et al. emphasize that in coastal systems, aligning engineering, and ecological objectives can deliver a wide range of benefits. However, it is necessary to assess how ecosystem-based approaches contribute to the resilience of coastal systems. They have developed and demonstrated an assessment rubric for Engineering With Nature® projects and they discuss its limitations and ways forward.

The papers in this Research Topic illustrate how ongoing work to operationalize ecological resilience concepts is improving strategic, multi-scale approaches for managing ongoing change to global ecological systems. Increased understanding of the ability of focal systems to maintain fundamental structures, processes, and functioning in the face of disturbances and stressors is being used to identify the relative ecological resilience of ecosystems and impending transitions to alternative states. New geospatial data, tools, and models are allowing assessments of resilience from broad to local scales that can be used to target both restoration and conservation activities, and to determine the most appropriate management strategies. And approaches that explicitly address the socioecological complexities and multi-scaled structure in systems show great promise in helping ecosystems and the communities that depend on them adapt to ongoing change. Clearly, resilience-based management in the Anthropocene will require new or stronger laws, policies, or guidelines. To ensure that resilience-based approaches to management are developed and applied to conserve and restore ecosystems effective collaboration among managers, scientists, and communities is a requisite.

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JC, CA, and SC wrote and edited the article.

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Discontinuity Analysis Reveals Alternative Community Regimes During Phytoplankton Succession

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It is well-recognized in plankton ecology that phytoplankton development can lead to distinct peaks (i.e., blooms) during spring and summer. We used a 5-year (2007–2011) phytoplankton data set and utilized discontinuity analysis to assess resilience attributes of spring and summer blooms based on the cross-scale resilience model. Using the size structure (i.e., cross-scale structure as an indicator of resilience) in the sampled plankton data, we assessed whether spring and summer blooms differ substantially between but not within blooms; that is, whether they comprise alternative community regimes. Our exploratory study supported this expectation and more broadly resilience theory, which posits that ecological systems can manifest in and change between alternative regimes. The dynamics of regimes receives increased attention because rapid environmental change potentially irreversibly alters ecosystems. Model organisms are needed that allow revealing patterns and processes of various aspects of regime dynamics at tractable time scales. Our preliminary findings suggest that phytoplankton can be suitable models for assessing the intricacies of regimes and regime changes.

Keywords: Baltic Sea, resilience, cross-scale structure, phytoplankton, blooms, alternative regimes, discontinuities, community succession

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INTRODUCTION

Patterns of discrete size structures of organisms in communities are related to a number of abiotic and biotic factors that operate across distinct scales of space and time; that is, they reflect the hierarchical organization of ecosystems (Nash et al., 2014; Sundstrom et al., 2018). This is due to competitive interactions and behavioral, life-history, and morphological adaptations to resources (e.g., food and shelter) that prevail at each scale (Holling, 1992; Segura et al., 2013). For instance, an elephant and an ant in a savannah interact with and exploit very different scales in the system. The discrete size structure within communities, also referred to as cross-scale structure (Sundstrom et al., 2018), has been suggested to serve as a surrogate of resilience in ecosystems (Angeler et al., 2016), and other complex systems (Sundstrom et al., 2014). This is due to the ability of one scale (discrete size structure) in the system being able to buffer against disturbances at other scales as a function of their functional trait characteristics and diversity (Angeler and Allen, 2016).

Resilience theory posits that ecological systems undergo substantial reorganization when they shift between alternative regimes (Angeler and Allen, 2016). Spanbauer et al. (2016) showed that the discrete size structure of benthic diatoms in Foy lake (USA) substantially

changed as a result of a regime shift. This is consistent with predictions that cross-scale structure as an indicator of resilience can identify regimes and regime changes (Baho et al., 2017). Phytoplankton communities are both discontinuously structured (Segura et al., 2013; Downing et al., 2014) and they can undergo substantial seasonal reorganization (e.g., Sommer et al., 2012; Behrenfeld and Boss, 2014). For instance, in the Baltic Sea phytoplankton communities show multiple seasonal peaks ("blooms"). These blooms have been shown to undergo repeated cycles of reorganization and collapse, which from a resilience perspective suggest community-level regime shifts (Angeler et al., 2015). However, it is still unclear if these dynamics reflect the manifestation of and change between alternative regimes posited by resilience theory. Therefore, research is needed to address this question, especially to shed light on potential similarities and differences between resilience-based approaches and taxonomic studies that have dominated research agendas in ecology in the past.

Phytoplankton is potentially a useful model for studying alternative community regimes because they have fast turnover, communities have high species diversity, and they show complex system dynamics (Leibold and Norberg, 2004). This behavior is influenced by feedbacks that emanate from interacting biotic (trophic cascades and competition) and abiotic (stratification, nutrients, temperature) variables (Sommer et al., 1986; Leibold and Norberg, 2004). These dynamics are well-documented in ecology, particularly ecological succession, and plankton ecology (Clements, 1916; Sommer et al., 2012). These paradigms are therefore valuable for assessing alternative community regimes, based on the cross-scale structure present in the study system. Phytoplantkon communities develop into spring and summer blooms and in relation to a spring clear-water phase (Sommer et al., 1986; Hajdu, 2002), although these patterns can vary among ecosystems (Jaanus et al., 2011). In our study system, the Baltic Sea, spring blooms develop from March to May and summer blooms occur between June and August (Angeler et al., 2015). These blooming periods are stable and recur annually, although there is annual variation in bloom timing. This timing provides an opportunity to assess whether spring and summer blooms comprise alternative phytoplankton community regimes.

In the Baltic Sea, spring blooms are the result of several factors. Among those are seasonal increases in temperature and solar radiation. Temperature and saline gradients that lead to stratification after winter mixing can also be important. At the beginning, spring blooms, which are characterized by high biomass, are dominated by diatoms that grow fast and later replaced by dinoflagellates with slower growth. With increasing temperature increase and nutrient depletion, spring blooms collapse, and reorganize in species-rich summer blooms with many inedible flagellates and cyanobacteria (Angeler et al., 2015). This reorganization is partly the result of changing food webs that alter biotic feedbacks; specifically, top-down effects, including zooplankton grazing that shapes the dynamics of phytoplankton (Sommer et al., 1986, 2012). In addition, Baltic Sea phytoplankton shows variability in taxonomic structure and the phenology of blooms (Jaanus et al., 2011; Klais et al., 2011; Suikkanen et al., 2013), which results from the interaction of anthropogenic (eutrophication, overfishing), climatic, and biotic factors (Elmgren, 1989; Wasmund and Uhlig, 2003; Österblom et al., 2007). Complex interactions between winter temperature and nutrient dynamics further affect community responses during spring and summer (Janssen et al., 2004).

The seasonally recurring spring and summer blooms that reflect phytoplankton dynamics allow for assessing assumptions regarding community dynamics during different successional stages. In this exploratory study, we assess cross-scale structure in spring and summer phytoplankton blooms to test the following expectations:

Phytoplankton blooms across seasons represent alternative regimes, reflected in different cross-scale structure, because of differing abiotic and biotic conditions between both bloom seasons.

During the duration of individual blooms, cross-scale structure between sampling events should not be significantly different as a result of the intrinsic regime properties that organize community dynamics within each bloom.

MATERIALS AND METHODS

Ethics Statement

All field and laboratory work is approved by the Swedish Agency for Marine and Water Management (HaV) and are part of the Baltic Sea Monitoring Program. Data used in this study are available through the Swedish Meteorological and Hydrological Institute (SMHI) and the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.8hj8t). No endangered or protected species were involved in this study.

Sites and Sampling

Phytoplankton communities were assessed at the 40 m deep B1 station near the coast of Askö (58°48′ N, 17°38′ E) and at the 459 m deep BY31 offshore station at Landsort Deep (58°35.90′ N, 18°14.21′ E). These sites are located in the southern area of the Baltic Sea, specifically in the NW Baltic Proper. Data were collected from both stations in weekly to fortnightly intervals in spring (March–May) and summer (June–August) between 2007 and 2011. Sampling and analysis adhered to standardized protocols. Phytoplankton samples were taken as integrated samples with a sampling hose (inner diameter 19 mm) from 0 to 20 m and preserved with acid Lugol's solution (Willén, 1962). In this way we could integrate abiotic and biotic heterogeneity in the water column and more accurately capture bloom aspects over the spring and summer. Taxonomic experts carried out the evaluation of phytoplankton adhering to standard protocols. Briefly, an inverted microscope with phase contrast was used to count phytoplankton (>2 um) after sedimentation in 10- or 25-mL chambers. Cells were measured and their sizes classified following HELCOM (2008). Carbon content was calculated from the biovolume of all individuals of a species, including colonial taxa. These evaluations were carried out following Olenina et al. (2006) and standardized volumes (http://www.ices.dk/marine-data/vocabularies/Documents/PEG_BVOL.zip).

Statistical Analyses

We used discontinuity analysis for assessing the cross-scale structure present in the phytoplankton communities (Barichievy

et al., 2018). The evaluation of cross-scale structure has been originally based on animal body sizes (Holling, 1992). More recently it has been extended to a broader discontinuity framework that accounts for abundances in ecological studies (Angeler et al., 2014; Sundstrom et al., 2018) and that accommodates metrics from non-ecological systems (e.g., city size: Garmestani et al., 2008). There is also evidence that plankton studies based on body mass of single species and biovolume of populations give similar results (Baho et al., 2015). In this study we used volumetric data and assessed cross-scale structure in the carbon content of phytoplankton using Bayesian Classification and Regression Trees (BCART) (Chipman et al., 1998). Phytoplankton carbon content was rank ordered based on ascending log-transformed measures of individual populations in the communities. Rank-ordered matrices were created for each phytoplankton community at each sampling date during the study period. BCART was conducted individually on these matrices to identify biomass groups in the phytoplankton community data for each sampling date by assessing within-group homogeneity (Stow et al., 2007). The analysis was based on a million iterations repeated 25 times. From this universe of trees the best 20 were displayed and the tree with the best (highest) log-likelihood ratio was selected for further analysis. The trees branch into distal nodes that comprise groups with highest homogeneity. In our study, these homogeneity groups are composed of phytoplankton populations that differ between groups in terms of their homogeneities in carbon content, and they likely emerge from the patterns-process relationships present within each bloom regime (Holling, 1992; Allen et al., 2005; Angeler et al., 2012). That is, the homogeneity groups identified by the BCART trees were used for classifying the phytoplankton populations into aggregation groups, thereby determining the cross-scale structure in the community. These homogeneity or aggregation groups were used to calculate nine diagnostics of phytoplankton cross-scale structure in carbon content for further analysis. These diagnostics are rooted in and therefore represent individually and collectively the cross-scale resilience model (Peterson et al., 1998), a commonly applied tool for quantifying resilience (Angeler and Allen, 2016). These diagnostics are: (1) total number of aggregation groups for the phytoplankton community at each sampling date, (2) the average of their aggregation group lengths (each aggregation length was measured as the difference between the lowest and highest log-transformed carbon content of a specific aggregation group), (3) averages of gap lengths (each gap length was measured as the difference between the log-biomass value of edges between adjacent aggregation groups), (4) standard deviation of aggregation lengths within a community as a variability measure of aggregation lengths in the community, (5) standard deviations of gap lengths, (6) average number of phytoplankton species composing carbon content aggregation groups of each analysis, (7) standard deviation of species composing aggregation groups, (8) lowest carbon content, and (9) highest carbon content values for each community were used for bounding the other diagnostics according to carbon content ranges of the phytoplankton communities.

Permutational multivariate ANOVA (PERMANOVA) (Anderson, 2005) was used to contrast the diagnostics of phytoplankton biomass cross-scale structure following the design of Angeler et al. (2015). The PERMANOVA model had three main terms. Factor 1 (Blooms) was fixed and contrasted blooms between spring and summer based on average cross-scale structure of phytoplankton. Factor 2 (Years) was random and categorical and comprised the study years from 2007 to 2011. Factor three (Months nested in years) was also random and comprised within-bloom dynamics during spring (March,

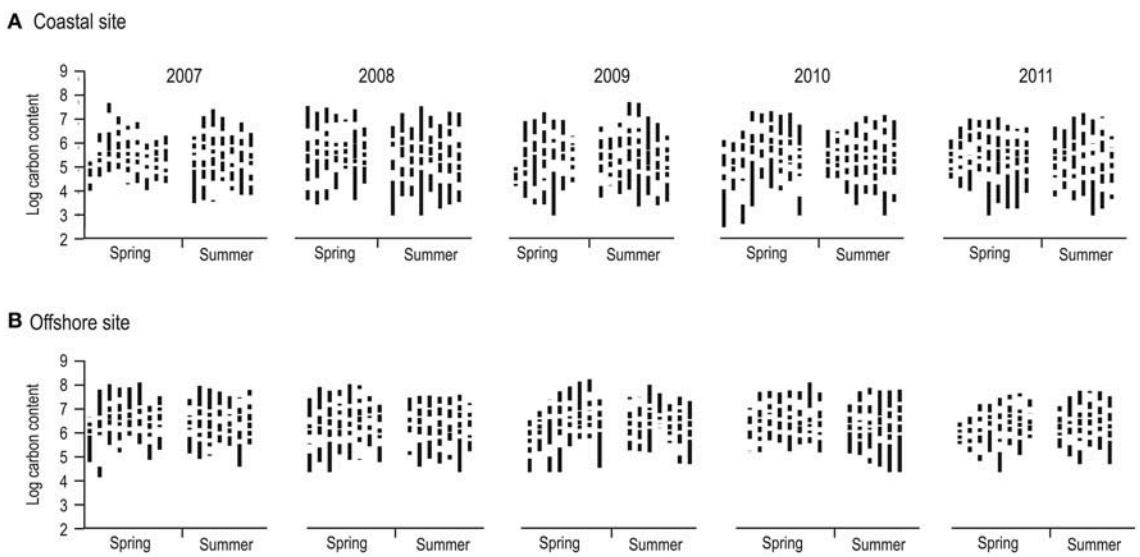

FIGURE 1 | Phytoplankton cross-scale structure during spring and summer blooms at a coastal **(A)** and offshore **(B)** site between 2007 and 2011 in the Baltic Sea. Shown are stacked biomass aggregation groups (black bars; ranges from lowest to highest biomass within a group) separated by gaps (white bars; no biomass present between aggregation groups) during repeated (8–9) sampling events within blooms.

April, May) and summer (June, July, August). Interaction terms between these factors were also tested. Three terms allowed assessing whether phytoplankton communities organize in distinct spring and summer community regimes in the Baltic Sea under our study period: (1) The term "Blooms" tests if phytoplankton cross-scale structure differs between spring and summer. This term is expected to be significant if spring and summer blooms comprise alternative community regimes. (2) The interaction term "Blooms × Months (Years)" assesses dynamic change of cross-scale structure within blooms. Because individual blooms are considered alternative community regimes, cross-scale structure between sampling events should not be significantly different due to regime-inherent properties that steer community dynamics within each bloom (Angeler et al., 2015). (3) The interaction term "Blooms × Years" tests if diagnostics of cross-scale structure are stable during spring and summer over the study years. If phytoplankton organizes in different spring and summer alternative community regimes consistently over time this term is not expected to be significant. PERMANOVA was calculated on Euclidean distance matrix of

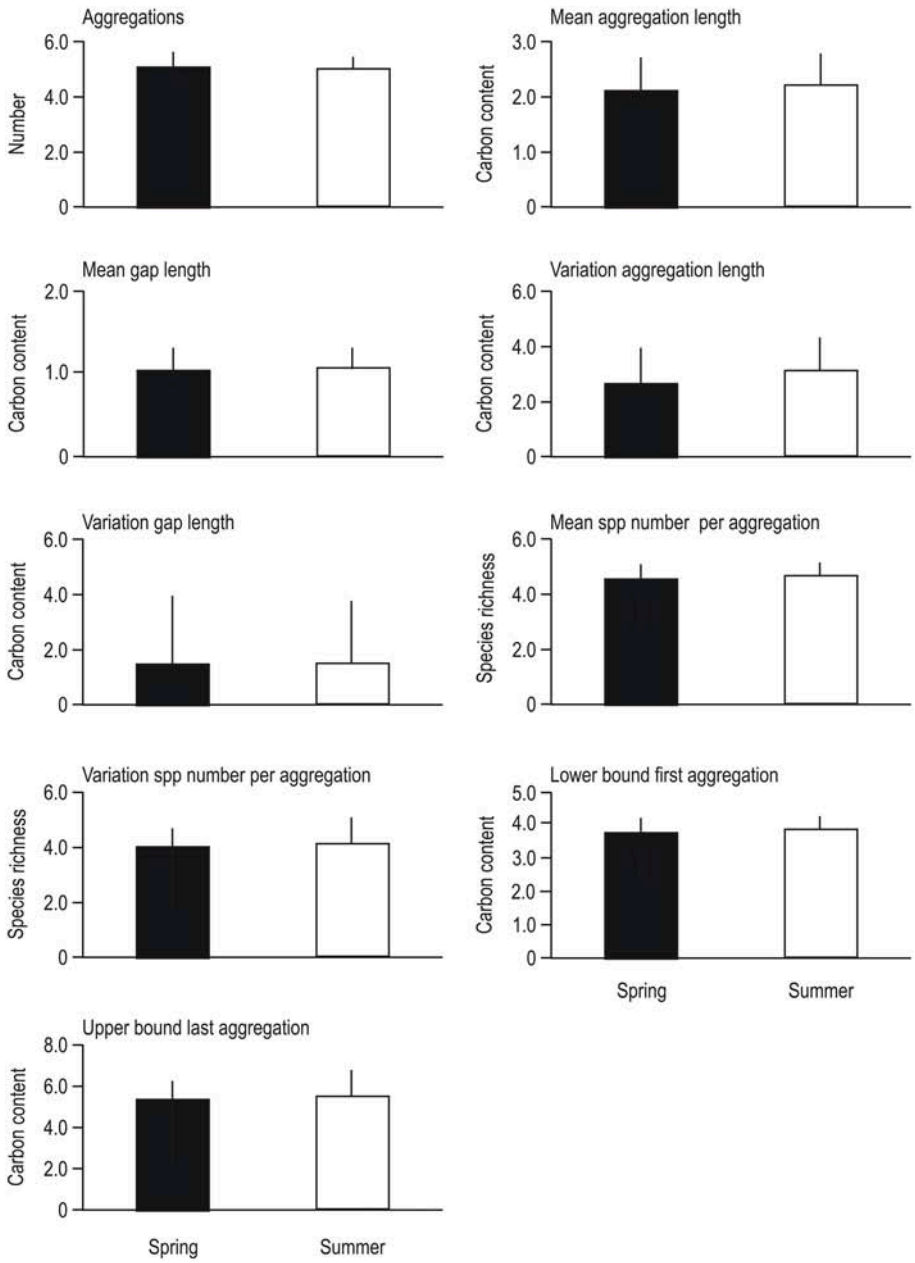

FIGURE 2 | Comparison of resilience metrics based on the cross-scale resilience model used for analysis. Shown are the means and standard deviations from 3 yearly measurements for each site (coastal and offshore) for the study period 2007–2011 ($n = 36$). See section Materials and Methods for descriptions and calculations of these metrics.

standardized diagnostics of phytoplankton biomass cross-scale structure using the coastal and offshore sites as replicates. Nine thousand nine hundred and ninety-nine unrestricted permutations of raw data were used and calculations were carried out with PERMANOVA v1.6 (Anderson, 2005). Significance testing was based on Monte Carlo asymptotic *P*-values.

RESULTS

Phytoplankton community cross-scale structure showed substantial variation between and within blooms between 2007 and 2011 at the coastal and offshore site in the Baltic Sea (**Figure 1**). Examining visually individual resilience metrics used for analysis revealed subtle differences between spring and summer blooms, with the exception of the variation (standard deviation) in the length of aggregations (i.e., the difference between the lowest and highest log-transformed biomass of a specific aggregation group), which was higher in summer compared to spring blooms (**Figure 2**). Despite the apparent similarities observed in individual metric comparisons and the variability in the data set, PERMANOVA detected a significant "Blooms" effect (**Table 1**). This suggests that phytoplankton cross-scale structure may reorganize in alternative community regimes between spring and summer. The effect of "Years" (study period between 2007 and 2011) was not significant, highlighting that the phytoplankton cross-scale structure of blooms is not changing during the study period. The insignificant interaction term "Blooms × Years" highlights that phytoplankton cross-scale structure present during spring and summer blooms remains differentiated over the study period. Finally, the term "Blooms × Months (Years)" was not significant. This suggests similar cross-scale structure between sampling events within each regime.

DISCUSSION

The results of our exploratory study show that phytoplankton seasonal development reflects the organization into alternative regimes, consistent with ecological resilience theory. This finding aligns with a previous study that assessed patterns of bloom collapse and reorganization following the adaptive cycle (Angeler et al., 2015), a heuristic of complex system change (Holling, 1986; Gunderson and Holling, 2002). The results are also in agreement with a plethora of taxonomic studies in marine (Edwards and Richardson, 2004; Lindemann and St John, 2014; Vidal et al., 2017) and freshwater (Sommer, 1985; Munawar and Munawar, 1986; Reynolds, 2006) environments that have documented substantial community changes in terms of phytoplankton species composition and biomass as a result of abiotic variability.

Although our results need to be interpreted with caution due to low sample size and heterogeneity of sites, the significant "blooms" term in the PERMANOVA model preliminarily supports the interpretation that spring and summer blooms generally comprise alternative phytoplankton community regimes. Alternative regimes are usually associated with ecosystem dynamics (e.g., Beisner et al., 2003); however, alternative regimes at the community level, which are often transient, have also been documented (Fukami and Nakajima, 2011; Jiang et al., 2011). Such changes can occur when variability at the ecosystem level creates abiotic and biotic conditions that entail a substantial restructuring at lower hierarchical levels in the system; i.e., at the scale of ecological communities (Allen et al., 2014). Such reorganization was the case in our study. Although the Baltic Sea is considered to operate in a stable eutrophic regime (Yletyinen et al., 2017), the substantial seasonal changes in the abiotic and biotic environment can lead to a transitioning of phytoplankton communities between alternative regimes. In the Baltic Sea, abiotic changes are related to temperature, nutrients, stratification, and salinity (Angeler et al., 2015). Biotic changes are manifested in alterations of food webs; i.e., trophic cascades including zooplankton grazing affect the dynamics of phytoplankton assemblages (Winder and Cloern, 2010; Sommer et al., 2012; Behrenfeld and Boss, 2014).

Most phytoplankton successional studies are based on taxonomic analyses. These studies show high community turnover between spring and summer blooms and also a high replacement of species and major taxonomic groups from the onset to the end of blooms (Reynolds, 2006). For instance, in the Baltic Sea dinoflagellates replace initially dominant diatoms toward the end of spring blooms. Similarly, summer blooms are characterized by a dynamic replacement between cyanobacteria, cryptophytes, and dinoflagellates (Angeler et al., 2015). These changes are due to functional attributes of phytoplankton species with some species (diatoms) being r-strategists; that is, they grow fast when nutrient availability is high (Sommer, 1981). On the other hand there are some species that are K-strategists, which characterize slow growing species (dinoflagellates) that are competitively weaker compared to diatoms, and that become abundant during periods of low nutrient availability (Sommer, 1981; Lembi and Waaland, 2007).

Using cross-scale structure in the carbon content of phytoplankton populations in the discontinuity analysis rather than taxonomic information, our results show an important difference between both approaches. A previous taxonomy based study using the same data set, which thus allows for direct comparisons, found significant within-bloom variability in phytoplankton community composition (Angeler et al., 2015).

TABLE 1 | Results of PERMANOVA analysis contrasting multivariate cross-scale structure across blooms (averaged spring and summer blooms of phytoplankton), years (2007–2011), months nested in years (3 months comprising each bloom), and their interactions.

Factor	df	SS	MS	F	*P*
Blooms	1	0.06	0.06	7.40	**0.004**
Years	4	0.16	0.04	1.42	0.193
Months (Years)	10	0.28	0.03	1.69	**0.023**
Blooms × Years	4	0.03	0.01	0.44	0.951
Blooms × Months (Years)	10	0.19	0.02	1.19	0.258
Residual	30	0.49	0.02		
Total	59	1.21			

Shown are degrees of freedom (df), sums of squares (SS), mean squares (MS), F-ratios (F), and the Monte Carlo asymptotic P-values (P). Significant P-values are highlighted in bold.

However, such an effect was not detected using the cross-scale structure of carbon content in this study. Both findings are not mutually exclusive. Taxonomic studies capture the pronounced abiotic and biotic variability within blooms while cross-scale structure as a measure of system resilience provides a more conservative, systemic measure of relative stability, and persistence of a regime. In this context stability and persistence are defined as the regime dynamics that are bound within a basin of attraction (Angeler and Allen, 2016). Specifically, alternative regimes are characterized by patterns-process relationships and feedbacks that are relatively stable (Beisner et al., 2003), although variability occurs within a regime when they adapt and cope with disturbances (Gunderson, 2000; Angeler et al., 2019). Such variability is clearly evident in the dynamics of cross-scale patterns within spring and summer regimes (**Figure 1**), which may reflect adaptive community dynamics within the basins of attraction of spring and summer blooms.

We conclude with acknowledging that we could only use two sites for this study, which prevents us from drawing firm conclusions about phytoplankton dynamics in the Baltic Sea. However, the exploratory results allow us to highlight the potential to study plankton seasonality from a resilience perspective. Accounting for the complexity inherent in resilience might potentially contribute to a better understanding of ecosystem dynamics and potentially management (Angeler et al., 2014). Specifically, our preliminary findings broadly supported resilience theory, which posits that ecological systems can manifest and change between alternative regimes. The dynamics of regimes receive increased attention by scientists and managers because rapid environmental change potentially irreversibly alters ecosystems. Model organisms are needed that allow revealing patterns and processes of various aspects of regime dynamics at tractable time scales. Our findings suggest that phytoplankton can be suitable models for assessing the intricacies of regimes and regime changes repeatedly over relatively short time spans.

AUTHOR CONTRIBUTIONS

DA conceived and designed study, carried out analysis, and wrote the paper. CA, DT, and MW contributed to idea development and the writing. All authors provided funding and approved submission.

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Operationalizing Resilience and Resistance Concepts to Address Invasive Grass-Fire Cycles

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Plant invasions can affect fuel characteristics, fire behavior, and fire regimes resulting in invasive plant-fire cycles and alternative, self-perpetuating states that can be difficult, if not impossible, to reverse. Concepts related to general resilience to disturbance and resistance to invasive plants provide the basis for managing landscapes to increase their capacity to reorganize and adjust following fire, while concepts related to spatial resilience provide the basis for managing landscapes to conserve resources and habitats and maintain connectivity. New, spatially explicit approaches and decision-tools enable managers to understand and evaluate general and spatial resilience to fire and resistance to invasive grasses across large landscapes in arid and semi-arid shrublands and woodlands. These approaches and tools provide the capacity to locate management actions strategically to prevent development of invasive grass-fire cycles and maintain or improve resources and habitats. In this review, we discuss the factors that influence fire regimes, general and spatial resilience to fire, resistance to invasive annual grasses, and thus invasive grass-fire cycles in global arid and semi-arid shrublands and woodlands. The Cold Deserts, Mediterranean Ecoregion, and Warm Deserts of North America are used as model systems to describe how and why resilience to disturbance and resistance to invasive annuals differ over large landscapes. The Cold Deserts are used to illustrate an approach and decision tools for prioritizing areas on the landscape for management actions to prevent development of invasive grass-fire cycles and protect high value resources and habitats and for determining effective management strategies. The concepts and approach herein represent a paradigm shift in the management of these ecosystems, which allows managers to use geospatial tools to identify resilience to disturbance and resistance to invasive plants in order to target conservation and restoration actions where they will provide the greatest benefits.

Keywords: non-native invasive grasses, fire regimes, resilience to fire, resistance to invasive plants, spatial resilience, high value resources, prioritization, management strategies

INTRODUCTION

Plant invasions are a global problem that affect ecosystems in a wide variety of ways. One of the most significant impacts to terrestrial ecosystems is when invasive plants affect fuel characteristics, fire behavior, and ultimately fire regimes (D'Antonio et al., 1992; Brooks et al., 2004). When invasive plants alter fire regimes in ways that promote their own persistence and dominance over native plant species, an invasive plant-fire cycle can establish (Brooks et al., 2004). The result is often alternative, self-perpetuating states that can be difficult, if not impossible, to reverse. These novel, alternative states are typically characterized by a general decline in resilience to disturbance and resistance to subsequent plant invasions that can spiral into an invasional meltdown (Simberloff and Von Holle, 1999).

One of the most effective ways to prevent landscapes from spiraling into decline is to prevent the initial development of invasive plant-fire cycles. Concepts related to general resilience to disturbance and resistance to invasive plants provide the basis for managing landscapes to increase their capacity to reorganize and adjust following fire and interacting disturbances and stressors, such as climate change (see **Table 1** for definitions) (Chambers et al., 2014a, 2016; Curtin et al., 2014). Concepts related to spatial resilience provide the basis for managing landscapes to conserve resources and habitats and maintain connectivity (Holl and Aide, 2011; Rudnick et al., 2012). Coupling information on resilience to fire and resistance to invasive plants with spatial resilience enables managers to evaluate how the potential for recovery and likelihood of invasive plant-fire cycles differ across large landscapes and how these differences can affect high value resources and habitats.

Recently, new approaches and decision-tools have emerged that enable managers to understand and evaluate general and spatial resilience to fire and resistance to invasive grasses across large landscapes in arid and semi-arid shrublands and woodlands (Chambers et al., 2014a,c, 2017a,c; Ricca et al., 2018)[1]. These spatially explicit approaches and tools provide the capacity to quantify and visualize differences in resilience and resistance across landscapes in relation to high value resources and habitats, fire risk, and presence and abundance of invasive grasses. This has resulted in a new paradigm that allows managers to locate invasive species management and fire preparedness, suppression, and prevention activities strategically, where they are likely to have the greatest benefits for maintaining and improving resources and habitats (Chambers et al., 2014a, 2017a,c; Ricca et al., 2018)[1].

Here we review our understanding of the factors that influence fire regimes, resilience to fire, resistance to invasive annual grasses, and thus development of invasive grass-fire cycles. We also discuss the factors that influence spatial resilience and the implications for high value resources and habitats. Our emphasis is on arid and semi-arid shrublands and woodlands in western North America. We use the Cold Deserts, Mediterranean Ecoregion, and Warm Deserts of North America as model systems to describe how and why resilience to disturbance and resistance to invasive annuals differ over large landscapes. We use the Cold Deserts to illustrate an approach and decision tools for prioritizing areas on the landscape for management actions to prevent development of invasive grass-fire cycles and protect high value resources and habitats.

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FIRE REGIME CHANGES AND DEVELOPMENT OF INVASIVE GRASS-FIRE CYCLES

Fire regimes are characterized by patterns of fire seasonality, frequency, size, spatial continuity, intensity, type (crown fire, surface fire, or ground fire), and severity in a particular area or ecosystem (Agee, 1994; Sugihara et al., 2006). Fire regimes in arid and semi-arid shrublands and woodlands are highly variable because they occur over large environmental gradients and differ in vegetation composition (Brooks and Matchett, 2006; Chambers et al., 2014a). The primary environmental and vegetation characteristics that influence fire regimes are climate, topography, soils, vegetation types, and plant functional groups (**Figure 1**). Fire occurrence in any given year is a function of several switches—fuels (biomass), the conditioning of those fuels for burning, fire weather, and ignitions (Archibald et al., 2009; Bradstock, 2010) (**Figure 1**). Changes in fire regimes can result from changes in the composition of plant functional groups (Syphard et al., 2017; Bradley et al., 2018), the amount and conditioning of biomass for burning (Littell et al., 2009), and ignitions, both human and lightening caused (Fusco et al., 2016). Fire size and intensity is strongly influenced by fire weather and fire behavior (Bradstock, 2010). Increases in atmospheric CO_2 concentrations that result in changes in climate and fire weather also have the potential to influence fire regimes (Littell et al., 2009; Abatzoglou and Kolden, 2013; Stavros et al., 2014) (**Figure 1**).

Fires in more arid shrubland and woodland vegetation types with low amounts of widely dispersed fuels are typically fuel-limited, because the amount and continuity of fuels are generally insufficient for fire to spread. One or more years of above-normal precipitation is often required to create sufficient fuel for large wildfires to burn (Crimmins and Comrie, 2004; Littell et al., 2009; Pilliod et al., 2017). In contrast, fires in less arid shrubland and woodland vegetation types with higher amounts of densely-packed fuels are often flammability-limited in that they have enough fuel to support fires every summer, but may not be dry enough to burn (Littell et al., 2009; Abatzoglou and Kolden, 2013). In these systems, warmer and drier conditions are often required to decrease fuel moisture sufficiently for large wildfires to burn. These two conditions represent endpoints of a continuum across large landscapes.

Non-native grass invasions can alter plant functional group composition and structure within vegetation types and thus the amount and availability of fuels across broad environmental gradients. These grasses create fine fuels that are highly flammable and their invasion increases both fuel loads and fuel continuity in fuel-limited systems, even at relatively low

TABLE 1 | Definitions used in this paper.

Ecological resilience: A measure of the amount of change needed to change an ecosystem from one set of processes and structures to a different set of processes and structures or the amount of disturbance that a system can withstand before it shifts into a new regime or alternative stable state (Holling, 1973). In the applied sciences, ecological resilience is also used as a measure of the capacity of an ecosystem to regain its fundamental structure, processes and functioning despite stresses, disturbances, or invasive species (Hirota et al., 2011; Chambers et al., 2014a; Seidl et al., 2016)
Fire regime: The patterns of fire seasonality, frequency, size, spatial continuity, intensity, type (crown fire, surface fire, or ground fire), and severity in a particular area or ecosystem (Agee, 1994; Sugihara et al., 2006). A fire regime is a generalization based on the characteristics of fires that have occurred over a long period
General resilience: A general and generic property of systems that describes the broad ability of a system to maintain fundamental structures, processes and functioning following disturbances (after Folke et al., 2010). General resilience is a function of environmental characteristics and ecosystem attributes and processes and is a useful concept for describing differences among ecosystems at landscape scales. The general resilience of an ecosystem is indicated by its ability to return to the prior or desired state and/or the recovery time after disturbances
Invasive plant species: An invasive species is (1) non-native (or alien) to the ecosystem under consideration, and (2) its introduction causes or is likely to cause economic or environmental harm or harm to human health (U.S. Presidential Executive Order 13112, 1999)
Spatial resilience: A measure of how spatial attributes, processes, and feedbacks vary over space and time in response to disturbances and affect the ecological resilience of the ecosystems that compose landscapes. Spatial resilience is a function of a landscape's composition, configuration, and functions
Resistance to invasive species: The abiotic and biotic attributes and ecological processes of an ecosystem that limit the population growth of an invading species (D'Antonio and Thomsen, 2004)

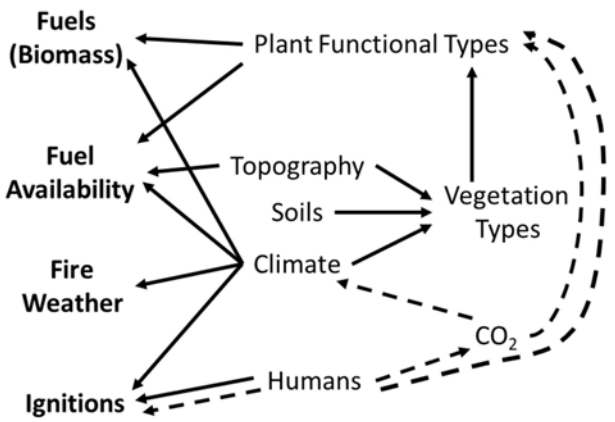

FIGURE 1 | Influences of abiotic and biotic factors (climate, soils, vegetation types, plant functional types) on fire regimes via four "switches" (fuels, fuel availability, fire weather, and ignitions). Potential effects of changing climate, human activity, and atmospheric CO_2 are indicated by dashed lines. Figure modified from Bradstock (2010).

abundances during their initial invasion (Bradley et al., 2018). Surface or near-surface fuels (primarily dead leaf material) facilitate the spread of fire in woodlands and shrublands around the globe, including Mediterranean shrublands of California (Syphard et al., 2017) and Chile (Gómez-González et al., 2011), Cold Desert shrublands in the western U.S. (Link et al., 2006), and most Australian vegetation types (Catchpole, 2002; Miller et al., 2010). Non-native grass invasions in arid and semi-arid shrublands and woodlands often result in invasive grass-fire cycles that support larger, more homogeneous, and more frequent fires (Syphard et al., 2017; Bradley et al., 2018). As a result of these invasions, fires are now becoming much more common in previously fuel-limited shrublands and woodlands where fires rarely occurred historically (Brooks et al., 2016). Fire frequencies that exceed the reproductive capacity of the dominant shrubs and trees can ultimately result in landscape conversion to invasive annual grass dominance (Miller et al., 2010; Pausas and Keeley, 2014), native or introduced forbs that are resilient to fire, or a mixture of both (Jones et al., 2018).

The amount and availability of invasive grass fuel varies across the landscape and is highly dependent on climatic/weather conditions. In arid and semi-arid shrublands and woodlands invaded by non-native grasses, wildfires tend to occur after one or more wet seasons or years and the accumulation of invasive grass fuels (Pilliod et al., 2017). Woody fuel loading and/or fine fuel loading interact with fire weather to influence the propensity for wildfires (**Figure 2**). As woody fuel loading and/or fine fuel loading increases, fuel packing ratios become more optimal, fuel continuity increases, and less severe fire weather is required for large wildfires. Invasive grasses increase fuel continuity and allow fires to burn under much lower fire weather severity than they would otherwise (**Figure 2**; Strand et al., 2014). Progressive increases in woody fuels due to management actions such as fire suppression also lowers the severity of fire weather required for large wildfires (e.g., Minnich, 2001), and can facilitate subsequent invasion of non-native grasses (Syphard et al., 2017). The length of the fire season and extreme fire weather conditions are projected to increase as the climate warms and may reduce the influence of fuel loads and continuity (Abatzaglou and Williams, 2016).

To determine if an invasive grass-fire cycle has established, it is necessary to: (1) document that a plant invasion has altered fuel bed characteristics; (2) demonstrate that these fuel bed changes alter the fire regime; and (3) show that the new regime promotes dominance of the fuels that drive the regime (D'Antonio et al., 1992). Rossiter et al. (2003) used indirect inference to test two assumptions of the invasive grass-fire model: (1) non-native grasses alter fuel load and ignitability; and (2) these changes increase frequency and/or intensity of fires (Rossiter et al., 2003). They showed that a perennial grass invader from Africa, *Andropogon gayanus* (Gamba grass), created fuel beds with seven times more biomass than those created by native Australian savanna species. This higher fuel load led to a fire that was eight times more intense than fires recorded in native fuel beds during the same time of year and produced the highest temperatures of any early dry season fire ever recorded in the Northern Territory, Australia. Although this study did not demonstrate that the invading species preferentially benefited from the fire behavior it created, numerous examples from other ecosystems suggest that

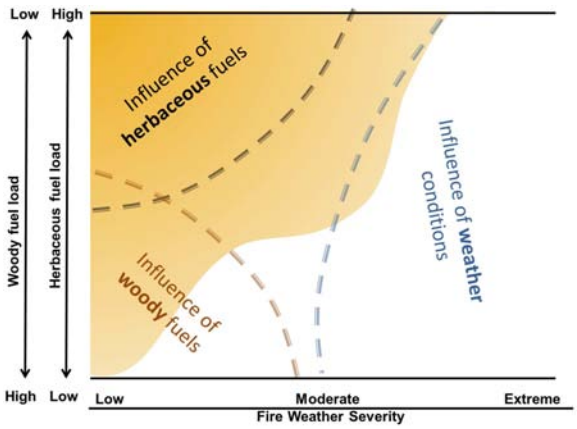

FIGURE 2 | A conceptual model of the interaction of herbaceous and woody fuels with fire weather severity. Fuel composition is displayed on the y-axis and fire weather condition is displayed on the x-axis. Low fire weather severity is characterized by high fuel moistures, high relative humidity, low temperature, and low wind speeds, while extreme fire weather is characterized by the opposite conditions. As woody fuel loading or fine fuel loading increases, fuel packing ratios become more optimal, fuel continuity increases, and less severe fire weather is required for large wildfires. Annual grasses produce fine fuels, represented by the area in yellow in the upper left, that can fill interspaces between native fuels (shrubs and grasses). Extreme fire weather conditions, which are projected to increase in the future, can override the influence of fuel loads and continuity. Figure modified from Strand et al. (2014).

African grasses typically benefit from frequent, moderate to high intensity fires (Brooks et al., 2004).

RESILIENCE TO WILDFIRE AND RESISTANCE TO INVASIVE GRASSES

General Resilience

The general resilience of ecosystems, or their broad ability to cope with disturbances (Folke et al., 2010) without changing regimes, differs among vegetation types and changes along environmental gradients in arid and semi-arid shrublands and woodlands. Ecosystem productivity and fuels generally increase over precipitation gradients. Seasonally arid vegetation types that produce more biomass have more frequent fires as illustrated for chaparral (Bond and Keeley, 2005) and sagebrush shrublands (Miller et al., 2013) in the western U.S., closed scrub to open mallee shrublands in Australia (Pausas and Bradstock, 2007; Bradstock, 2010; Miller et al., 2010), and Patagonian forests and shrublands (Mermoz et al., 2005). Areas with more frequent fires often have a higher proportion of plant functional types that are adapted to fire and thus capable of surviving and re-sprouting after fire (Mermoz et al., 2005; Pausas and Bradstock, 2007; Spasojevic et al., 2016). In relatively intact ecosystems, the combination of higher effective precipitation, greater productivity, and plant functional types adapted to fire typically results in greater resilience as indicated by smaller change in species composition following fire and more rapid return to the pre-fire community composition (Chambers et al., 2014a). Higher resource availability and plant productivity are associated with greater resilience to disturbance or recovery potential in the Cold Deserts (Condon et al., 2011; Davies et al., 2012; Chambers et al., 2014b, 2017b; Urza et al., 2017), Mediterranean Ecoregion (Corbin et al., 2007), and Warm Deserts (Brooks and Matchett, 2006).

The primary indicators of general resilience are environmental characteristics, including climate variables, topographic indices, and soil characteristics (**Table 2**). Ecosystem attributes and processes are also important factors in evaluating the general resilience of ecosystems (**Table 2**) and can include soil characteristics, land cover of vegetation types, productivity indices, species functional traits, and modeled attributes and processes, such as soil temperature and moisture regimes[2] ecophysiological processes (Levine et al., 2016), and successional process after fire (Spasojevic et al., 2016). For example, in the four-corner region of the USA, remote sensing, climate data, and species trait databases were used in path analyses to evaluate whether functional diversity across a range of woodland and forest ecosystems influenced general resilience as indicated by the recovery of productivity after wildfires (Spasojevic et al., 2016). Longer term data and climate change projections make it possible to assess state changes over time and evaluate the potential for climate induced thresholds (Littell et al., 2009; Abatzoglou and Kolden, 2013).

Resistance to Invasive Grasses

The potential for invasive grasses to alter fire regimes and ecological resilience is strongly influenced by the system's resistance to the invasive grass. Resistance to invasive grasses is determined by the species' fundamental and realized niche (Chambers et al., 2014a). The fundamental niche is a function of a species' physiological and life history requirements for establishment, growth, and reproduction, and is highly dependent on a system's environmental characteristics. Factors such as elevation, slope, aspect, and soil characteristics determine soil temperature and water availability and affect expression of the fundamental niche of invasive grasses at plant community to landscape scales (Brooks et al., 2016). Changes in fire regimes that affect environmental factors, like soil temperature and moisture regimes, and ecosystem attributes, like biogeochemical cycling, can also influence expression of the fundamental niche (Germino et al., 2016).

The realized niche is a subset of the fundamental niche and is determined largely by resource availability, biotic interactions with the plant community, and propagule pressure (Shea and Chesson, 2002). Niche opportunities can result when the life history of the invasive grass allows it to take advantage of "unused" resources within the plant community (Chambers et al., 2016; Germino et al., 2016). In many arid and semi-arid shrublands and woodlands, this is strongly influenced by the timing and amount of soil water storage, functional group dominance, and competitive interactions (**Figure 3**; Chambers

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TABLE 2 | The factors that contribute to general and spatial resilience to fire and resistance to invasive annual grasses and selected indicator variables for each factor.

Environmental characteristics	Ecosystem attributes and processes	Disturbances	Landscape context
Climate	*Abiotic*	*Ecosystem Disturbance*	*Landscape Composition*
- Precipitation	- Temperature and precipitation regimes	- Drought/Wet Periods	- Richness
- Temperature	- Hydrologic fluxes and water storage	- Fire	- Evenness
- Seasonality	- Geomorphic processes	- Plant Invasions	- Diversity
Topograhy	*Biotic*	*Anthropogenic Disturbance*	*Landscape Configuration*
- Elevation	- Biological productivity	- Agricultural, urban and energy development	- Patch size distribution and complexity
- Slope and Aspect	- Structure and composition	- Over harvesting	- Patch shape complexity
- Landform	- Functional groups, interactions, phenology and traits	- Improper grazing	- Core area
Soils	- Population regulation and regeneration	- Species introductions	- Isolation/proximity
- Depth and texture		- Nutrient enrichment, N deposition, acid rain	- Contrast
- %OM and nutrients		- Rising CO_2, climate change	- Contagion and interspersion
- pH		- Restoration and mitigation efforts	- Subdivision
			- Connectivity

et al., 2016). Native or desirable plant species that use similar resource pools and have resource use patterns that coincide with spatial or temporal aspects of the establishment and growth of invasive plant species are typically the most effective competitors (Leffler and Ryel, 2012). In systems that lack sufficient desirable plant species with resource use patterns similar to the invasive grass, reduced competition and higher resource availability can result in increased biomass, seed production, and spread of the invader (Chambers et al., 2007, 2017b; Olsson et al., 2012).

Disturbances like improper livestock grazing (timing, duration and/or intensity), altered fire regimes, and stressors such as rapid climate change, rising CO_2, and nitrogen deposition result in resource fluctuations that create niche opportunities and increase system invasibility (Davis et al., 2000; Davis and Pelsor, 2001; Shea and Chesson, 2002). The most common disturbances associated with decreased resilience and resistance in many arid and semi-arid shrublands and woodlands are improper livestock grazing and altered fire regimes (D'Antonio et al., 1992). Livestock grazing is a widespread land use in arid and semi-arid shrublands and woodlands that can alter plant functional types, biomass production, and thus fuel availability. Higher resource availability due to removal of perennial grasses and forbs by grazing can result in increases in woody species and fuel loads in shrublands and woodlands (Miller et al., 2013). Similarly, management actions, such as fire suppression, that reduce the range of natural variation (Holling and Meffe, 1996) can increase woody fuels in shrublands and woodlands that had shorter fire return intervals and lower levels of woody fuels historically (Minnich, 2001; Boyd et al., 2017). Larger and more severe fires that reduce abundance of woody species can create niche opportunities for invasive grasses.

Dispersal of invasive grass seeds and increased propagule pressure due to livestock grazing can result in increases in invasive grasses in interspaces among woody species and residual perennial grasses and forbs prior to wildfire (Reisner et al., 2013). Improper livestock grazing can also restrict native bunchgrasses to microsites under shrubs where fire intensity is greater and bunchgrass survival is less likely (Hulet et al., 2015). Higher or more contiguous fine fuel biomass can result in greater fire severity and extent, higher mortality of fire-intolerant trees, shrubs, and native grasses, and development of invasive grass-fire cycles (Pausas and Keeley, 2014). Biomass reduction of woody species for fuels management (mowing or removing shrubs, cutting down trees) can also increase resource availability and decrease resistance in areas that are climatically suited to invasive grasses, especially in sites that lack sufficient perennial natives for recovery (Prevey et al., 2010; Roundy et al., 2018).

Weather events and longer-term climate patterns can result in resource fluctuations that decrease resistance to invasion. Resource pulses due to weather events, such as above-average precipitation, can facilitate invasion where resource availability is greater than the capacity of the extant system to fully utilize the excess (Rejmanek, 1989; Davis et al., 2000). For example, extensive range expansion of *Pennisetum ciliare* (syn. *Cenchrus ciliaris*; buffelgrass) occurred in central Australia following periods of above-average rainfall in the mid-1970s and from 2000 to 2002 (Griffin et al., 1983; Friedel et al., 2006). This has been observed following El Niño years for *Bromus rubens* (red brome) in the Mojave Desert (Salo, 2005) and *Bromus tectorum* (cheatgrass) in salt desert vegetation types of the Cold Deserts (Meyer et al., 2001).

Progressive increases in CO_2 concentrations and minimum temperatures over recent decades are likely resulting in increases in invasive annual grasses, but effects appear to depend on environmental characteristics and resource availability and to be context specific. Recent research indicates that addition of CO_2 had positive effects on plant biomass in greenhouse studies (Ziska, 2005), no effect in a field study in the Wyoming Basin (Blumenthal et al., 2016), and depended on resource availability in the Mojave Desert (Nowak et al., 2004). Warming of minimum temperature by infrared heating had positive effects in areas of climate suitability for the invader (Campagnoni and Adler, 2014; Blumenthal et al., 2016), but warming by blocking convective cooling during days had no effect in areas at the limits of climate suitability (Larson et al., 2017).

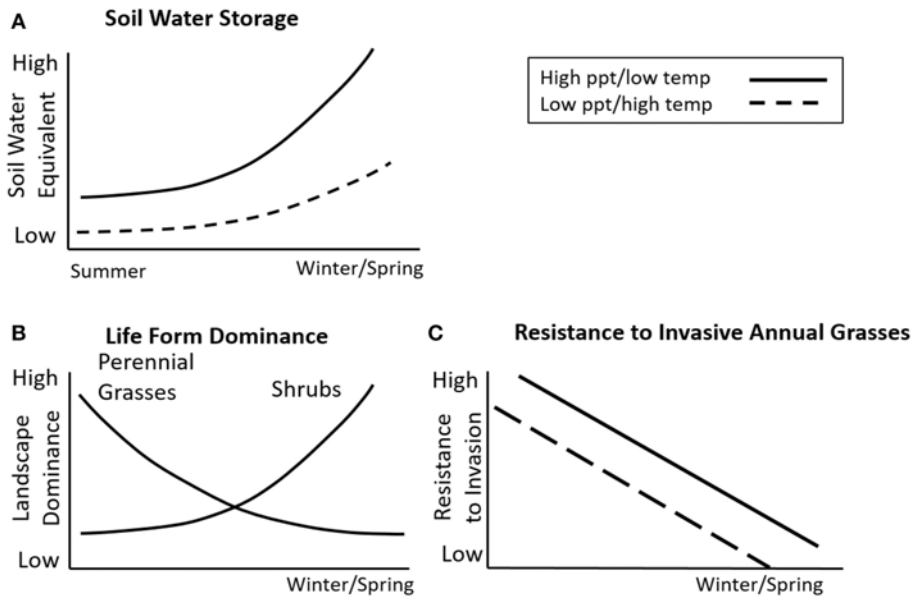

FIGURE 3 | Changes in soil water storage, life form dominance and resistance to invasive annual grasses as seasonality of precipitation transitions from primarily summer to winter in the Cold Deserts of western North America. **(A)** Soil water storage increases as the proportion of winter/spring precipitation increases and these changes are relatively greater for areas with relatively high precipitation and low temperature. **(B)** Landscape dominance of perennial native grasses is highest with primarily summer precipitation; shrub dominance is greatest with primarily winter/spring precipitation. **(C)** Resistance to invasive annual grasses is higher in areas where soil water storage is low and perennial grasses dominate largely due to strong resource competition. Decreases in effective precipitation can increase resource fluctuations and lower resistance to invasive annual grasses. At more local scales, resistance also is influenced by resource availability and disturbance. Figure modified from Chambers et al. (2016).

Many of the same environmental characteristics and ecosystem attributes that determine resilience to wildfire influence resistance to invasive species (**Table 2**). Envelope or niche models are used to model the potential habitat of invasive plants and often serve as the basis for assessments of invasion risk. These models use distribution data for invasive plants in combination with environmental correlates (typically climatic factors) to model potential habitat across large landscapes (e.g., Jiménez-Valverde et al., 2011; Vilà and Ibáñez, 2011; Bradley et al., 2013). Bioclimatic envelope models have been developed for several invasive grasses in arid and semi-arid shrublands and woodlands, including *P. ciliare* in northwestern Mexico (Arriaga et al., 2004) and *B. tectorum* in the western US (Bradley, 2009).

Remote sensing image analysis is increasingly used as a tool for mapping invasive plant species (Bradley, 2014; He et al., 2015) including after fire (West et al., 2016). The distinct cover, morphology and/or seasonality of many invaded vs. native ecosystems allows invasive species to be detected remotely. Inter-annual variability in phenology has been used to identify annual grasses in desert ecosystems, including *B. tectorum* (Boyte and Wylie, 2016) and *Eragrostis lehmanniana* (Lehmann lovegrass) (Huang and Geiger, 2008). Accurately detecting small populations in the early stages of invasion is difficult, yet maps of heavily infested areas increase information about temporal and spatial patterns and predictors of invasion and provide another valuable tool for risk assessment (Bradley, 2014). Innovation in technology has allowed the coupling of remotely sensed data with machine learning algorithms to map fractional (i.e., continuous) cover of plant functional groups (Anderson et al., 2018; Jones et al., 2018) and invasives (West et al., 2016). This has increased the ability to detect the early presence of invasives and to map ecosystem transitions. Maps of plant functional group percent cover, including annual grasses and forbs, are currently available annually at 30 m resolution for the western U.S. from 1984 to 2017 (Jones et al., 2018), and maps of *B. tectorum* have been produced at 250-m resolution for a portion of the Cold Deserts since 2000 (e.g., Boyte and Wylie, 2016).

Spatial Resilience

Spatial resilience is a measure of how spatial attributes, processes, and feedbacks vary over space and time in response to disturbances and affect the ecological resilience of ecosystems within landscapes. It is determined by the composition, configuration, and functions of patches within landscapes and is closely related to resilience to fire and resistance to invasive grasses. Spatial resilience considers the distribution of vegetation types, spatial connectivity among landscape patches, and thus the ability of fire (Miller and Urban, 2000; Peters et al., 2004) and invasive plants (Bradley, 2010; González-Moreno et al., 2014; Basnou et al., 2015) to spread within a landscape. Effects of human activities on patch connectivity are key considerations in spatial resilience because they impact fire regimes, plant invasions, and thus resources needed to support habitats and species populations (Holl and Aide, 2011; Leu et al., 2011; Rappaport et al., 2015). The capacity exists to delineate system

transitions by using fine resolution vegetation cover mapped across broad spatial and temporal scales (Jones et al., 2018).

At landscape scales, ignition and spread of wildfires result from complex interactions among topography, land cover, ignition sources, and weather (**Figure 1**). Wildfires start from a local epicenter (ignition point) and spread across landscapes as a function of the abundance and arrangement of disturbance-susceptible patches (Moreira et al., 2011). Fire spread rate can be facilitated or retarded by landscape heterogeneity. Thus, the spatial pattern of fire ignition and spread across landscapes are affected by fire proneness, i.e., the differential fire behavior in various land cover types that are not equally fire prone (e.g., Bajocco and Ricotta, 2008; Moreira et al., 2011).

Land use strongly affects fire risk by modifying vegetation structure and fuel loads, which, along with topography and weather, are the main drivers of fire intensity and rate of spread (Bradstock, 2010) (**Figure 1**). Thus, changes in land cover and land uses are directly linked to changes in landscape fuel patterns and fire risk (Moreira et al., 2011). Increased fire risk is expected where land use/land changes have promoted an increase in fuel loads, such as those resulting from expansion of trees into shrublands and shrubs into grasslands (Miller et al., 2013) or fuel continuity, such as those caused by annual grass invasions (Link et al., 2006). In contrast, other land uses or land cover changes can decrease fire risk when associated with the removal of biomass (e.g., targeted livestock grazing, fuel treatments) (Strand et al., 2014).

Wildland fire risk assessment and fuel management have become major activities in fire prone ecosystems as part of efforts to reduce the growing financial and ecological losses from wildfires (Ager et al., 2011; Scott et al., 2013; Chuvieco et al., 2014). Planners and fuel specialists routinely use simulation models to (1) characterize fire behavior under specific fuel and weather conditions, (2) examine potential effectiveness and ecological impacts of fuel treatment programs over a range of scales, from localized fuel types (5–50 ha) to large landscapes (1,000–50,000 ha), and (3) map fire risk to important social and ecological values (Collins et al., 2010; Ager et al., 2011). For example, wildfires are modeled to examine differences in wildfire probability and fire behavior across areas with high value conservation resources (national parks, species habitats) and to evaluate effects on wildlife habitat, soil erosion, and other factors (Scott et al., 2013). A wide variety of fire behavior models have been developed such as FlamMap, FARSITE, Behave, and FSIM along with supporting models and software to estimate appropriate weather, fuel moisture, and other input variables required to run the fire behavior models (see https://www.firelab.org/applications).

Complex interactions among climate, vegetation types, and human activity determine patterns of plant invasion across large landscapes. Land use related disturbances generally increase the likelihood of plant invasions (Gelbard and Belnap, 2003; Bradley, 2010). The risk of invasion can be evaluated based on spatial relationships among probabilities of grass invasion and land use variables, such as the distribution of roads, agriculture, and powerlines (Bradley, 2010; González-Moreno et al., 2014; Basnou et al., 2015). For example, spatial modeling was used to develop landscape-scale risk assessments associated with climate, land use variables, and invasion of *B. tectorum* for the State of Nevada in the U.S. (Bradley, 2010). In addition, relationships among climate, land use/land cover changes, and species invasions were evaluated for the Mediterranean region of Europe (González-Moreno et al., 2014; Basnou et al., 2015). Generalized linear models were used to examine effects of both current landscape structure and recent land use change from floristic surveys (species presence and relative abundance), climate and land cover variables, and human activity variables, and then to develop patch and landscape metrics of invasion.

RESILIENCE AND RESISTANCE OF WARM DESERTS, COLD DESERTS, AND MEDITERRANEAN ECOREGION

The arid and semi-arid ecosystems represented by the Cold Deserts, Warm Deserts, and Mediterranean Ecoregion (**Figure 4**) exhibit a wide range of temperature and precipitation regimes, which influences resilience to wildfire, resistance to invasive grasses, and the tendency for grass-fire cycles to develop (see review in Brooks et al., 2016). Differences in the aridity, amount, seasonality, and predictability of precipitation, and onset of the dry season influence plant functional type dominance and have important consequences for both fire regimes and grass invasions (**Figure 5A**). Aridity increases across a north to south gradient, with the Mojave Basin and Range and Sonoran Basin and Range being the most arid. Summer precipitation (July, Aug, Sept) increases across a west to east gradient with the Columbia Plateau, Snake River Plain, Northern Basin and Range, and entire Mediterranean Ecoregion receiving mostly winter precipitation, and the Sonoran Basin and Range, Arizona/New Mexico Plateau, and Chihuahuan Deserts receiving mostly summer precipitation (**Figure 5A**). The Central Basin and Range and Mojave Basin and Range are transitional and receive varying amounts of winter and summer precipitation. Amount of precipitation received when temperature, and thus potential evapotranspiration is low influences the amount of water stored in deep soil layers, and therefore the balance between woody and herbaceous plant species in these ecoregions (Sala et al., 1997; Wilcox et al., 2012). Areas that receive more winter/spring precipitation typically have deeper soil water storage and a higher proportion of shrubs (**Figure 6**). In contrast, areas that receive predominantly summer precipitation have little deep-water storage and a higher proportion of perennial grasses (**Figure 6**). Water availability during the period when temperatures are favorable for plant growth influences the balance between C3 and C4 species with C3 species dominating in areas with cool, wet springs and C4 species tending to dominate in areas with warm, wet summers (Paruelo and Lauenroth, 1996; Sala et al., 1997).

The occurrence of large fires is related both to the degree of aridity and the timing of precipitation (**Figure 5A**). Lower aridity equates to higher vegetation productivity and thus greater amounts and continuity of fuels, which leads to more frequent fires in shrubland ecosystems (Bond and Keeley, 2005; Bradstock, 2010). More winter/spring precipitation typically results in

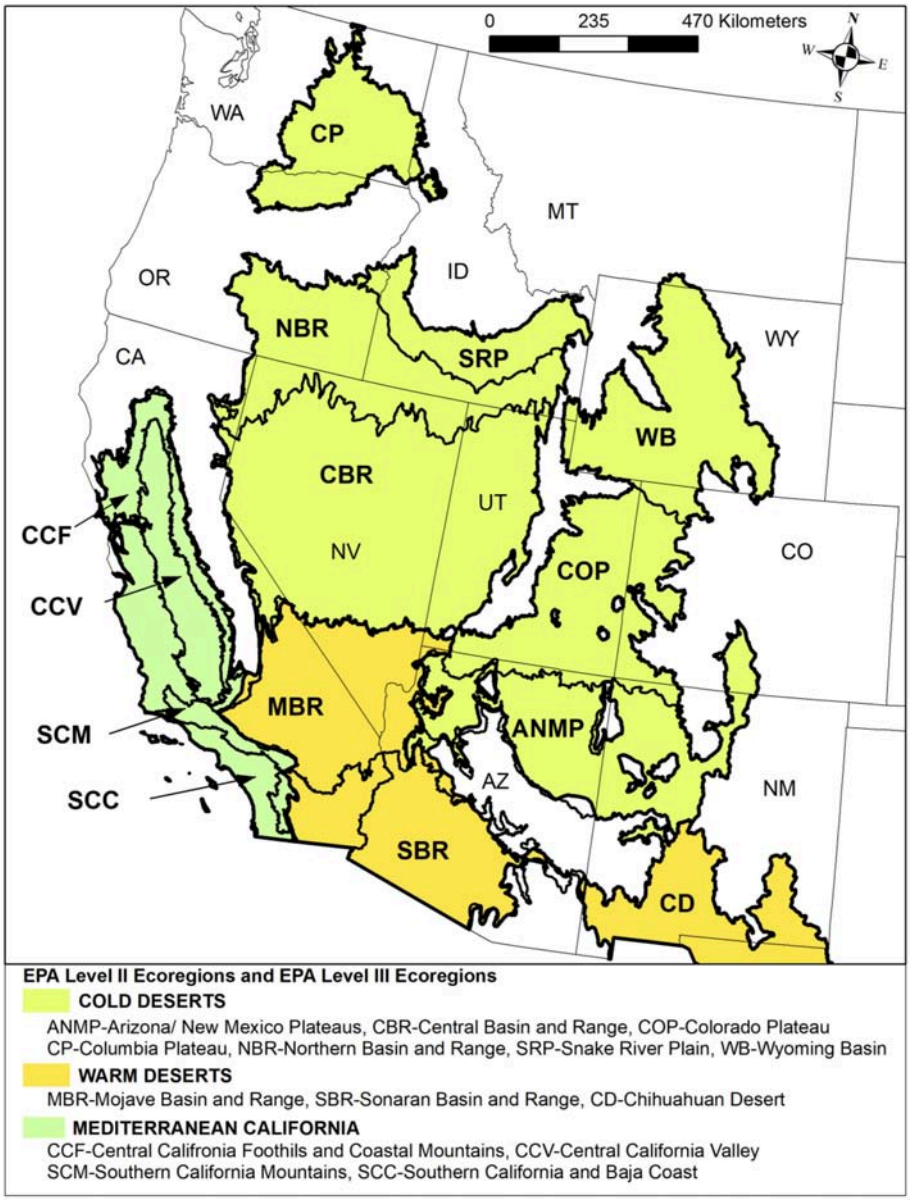

FIGURE 4 | A map of the Cold Deserts, Mediterranean Ecoregion, and Warm Deserts Level II Ecoregions in North America and the Level III Ecoregions within them (U.S. Environmental Protection Agency [USEPA]., 2017).

longer fire seasons in which most fires burn in June, July and August. These fires vary in size but can exceed 100,000 ha (Geo MAC Wildland Fire Support., 2018). Dominance of summer precipitation typically results in shorter fire seasons in which most fires burn earlier in the year, before the onset of summer rains (Littell et al., 2009; Abatzoglou and Kolden, 2013). These fires are typically smaller. Large fires have burned in the northeastern Mojave Desert, where precipitation is a mix of winter and summer precipitation and is highly variable (**Figure 5A**) (Tagestad et al., 2016; Brooks et al., 2018).

The likelihood of conversion to invasive grasses is also related to the degree of aridity and timing of precipitation (**Figure 5B**). Resistance to invasive annual grasses is generally lowest in areas with wet winters but increases with aridity due to less favorable conditions for establishment, or increasing summer rainfall, which is associated with strong competition from native perennial grass species (Bradford and Lauenroth, 2006; Bradley, 2009). Large percentage cover of invasive annual grasses and forbs, repeated wildfires, and extensive human development likely explain relatively low cover of shrubs and perennial forbs and grasses in the less arid portions of the Mediterranean ecoregion (Syphard et al., 2017). Similar factors explain relatively low cover of shrubs and perennial forbs and grasses in the Snake River Plain and

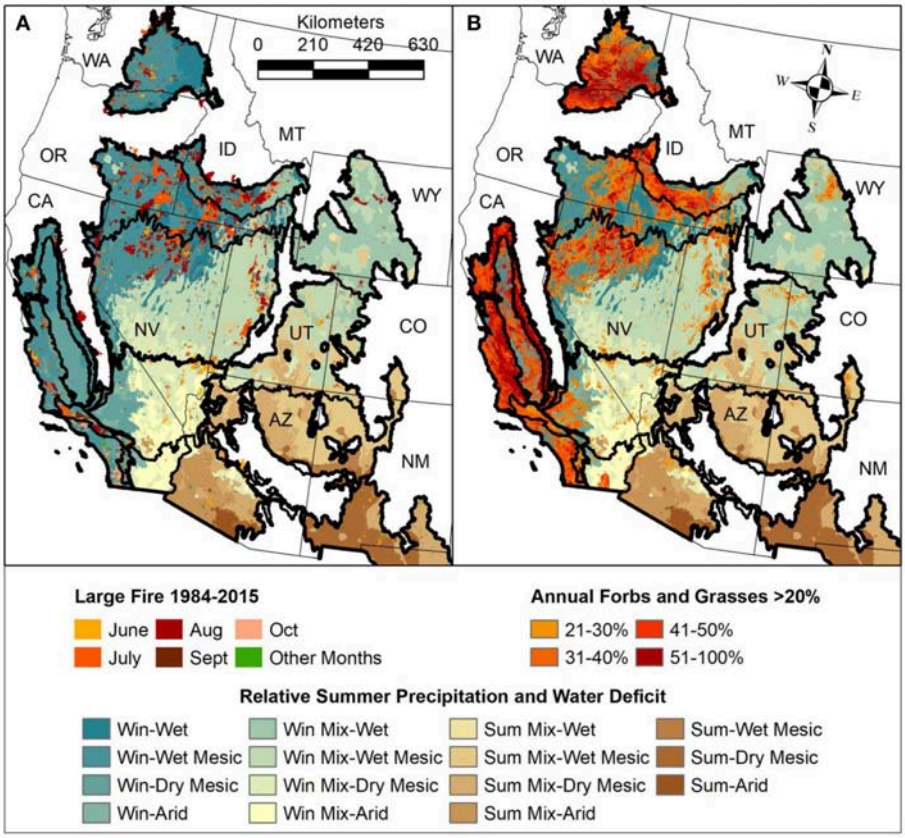

FIGURE 5 | A generalized aridity index (Dobrowski et al., 2013) combined with the timing of precipitation (winter or summer) based on 30-year normal annual values (PRISM Climate Group, 2016) and overlaid with **(A)** large fires in the months of June, July, August, September, October, and other months (1984–2015; Monitoring Trends in Burn Severity [MTBS], 2018) and **(B)** percentage cover of annual forbs and grasses derived from the per-pixel maximum values from 2015–2017 (Jones et al., 2018).

Northern Great Basin of the Cold Deserts (Knick et al., 2011; Balch et al., 2013).

Ecoregional Relationships

Prior sections show that effects of invasive grasses on fire regimes differ as a function of: (1) climatic regime and thus vegetation type; (2) plant functional groups and degree of fire adaptation of the vegetation type; (3) ecophysiological and life history characteristics of the invader; and (4) interactions with the dominant land uses and human developments. For planning and assessment, it is necessary to develop an understanding of how and why these factors differ in relation to relative resilience to fire and resistance to grass invasions. In the sections below, we discuss how these factors vary among the major vegetation types that comprise the Cold Deserts, Warm Deserts, and Mediterranean Ecoregion of the western United States.

Cold Deserts

General description

In the Cold Deserts, the dominant vegetation types occur along productivity gradients related to elevation and soil temperature and moisture regimes (**Figure 7**). Soil temperature regimes are predominantly warm (xeric) or cool (frigid) with small cold (cryic) areas at higher elevations and hot (thermic) areas in the south (Brooks et al., 2016). Soil moisture regimes range from winter moist (xeric; generally >30 cm annual PPT) to dry (aridic; generally <30 cm annual PPT) with large areas of dry and summer moist (aridic-ustic) in the Wyoming Basin and Colorado Plateau (Brooks et al., 2016). Salt desert vegetation types typically occur at lower elevations or in valley bottoms with drier soil moisture regimes and are dominated by members of the Chenopodiaceae, such as *Atriplex* spp. and *Sarcobatus* spp. (West, 1983a,b), but can include a diversity of shrub and grass species. *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) and to a lesser degree *A. tridentata* ssp. *tridentata* (basin big sagebrush) types are found at low to mid elevations with warm and dry to warm and moist soil temperature and moisture regimes (West, 1983a,b; Miller et al., 2011). *Artemisia tridentata* ssp. *vaseyana* (mountain big sagebrush) and mountain brush (e.g., *Symphoricarpos* spp. [snowberry.], *Purshia tridentata* [antelope bitterbrush]) types occur at upper elevations with cool and moist to cold and moist regimes (West, 1983a,b; Miller et al., 2011). Associated species differ

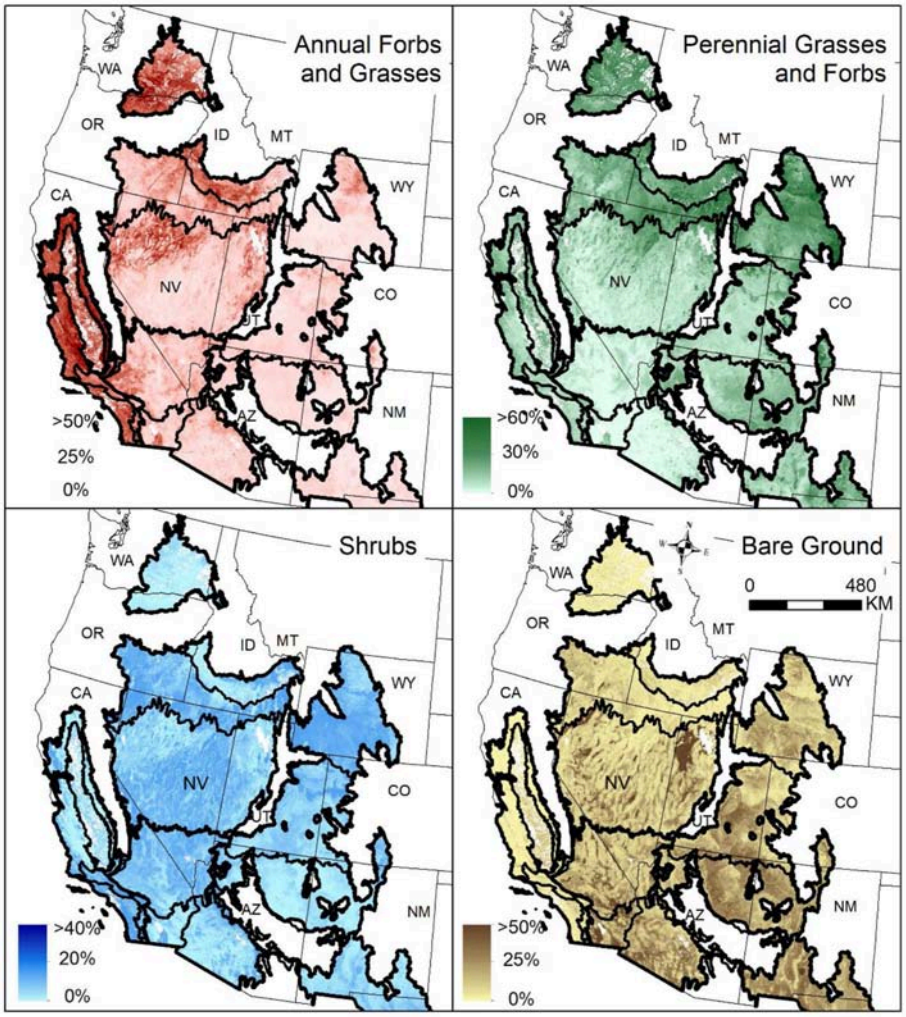

FIGURE 6 | Continuous land cover maps of annual forbs and grasses, perennial forbs and grasses, shrubs, and bare ground averaged for 2017 (modified from Jones et al., 2018). Water, snow/ice, cropland, developed, and wetland areas have been excluded using the National Land Cover Database (NLCD) (2014).

regionally, and the relative proportion of shrubs vs. herbaceous species can be highly dependent on grazing history and time since fire.

Resilience to fire

Resilience to fire increases along soil temperature, precipitation, and thus productivity gradients as observed in other arid and semi-arid shrublands (**Figure 7**) (Condon et al., 2011; Davies et al., 2012; Chambers et al., 2014a,b; Urza et al., 2017). In general, warmer and drier salt desert and Wyoming big sagebrush types have lower fuel biomass and availability and experienced few historical fires—fire return intervals varied regionally but were as long as 100 or more years (Miller et al., 2013). Consequently, these types have relatively low resilience to fire. In contrast, cooler and moister mountain big sagebrush and mountain big sagebrush/mountain shrub types are typically characterized by relatively high fuel biomass and availability and experienced more historical fires—fire return intervals also varied regionally but were as short as 10–12 years (Miller et al., 2013). These types have greater resilience to fire as indicated by more rapid post-fire recovery and smaller changes in species composition (Davies et al., 2012; Chambers et al., 2014b).

Resistance to invasion

The most problematic invasive grasses are winter annuals that are well-suited to those areas dominated by winter precipitation. These invasive annuals germinate in fall or spring, exhibit rapid growth, and are highly effective competitors for soil resources during spring to early summer (Chambers et al., 2007, 2016). Invasibility is closely related to soil climatic regimes as illustrated for the widespread invasive brome grasses, which are causing invasive grass-fire cycles (**Figure 7**) (Chambers et al., 2007, 2016, 2017b; Brooks et al., 2016). For example, germination, growth, or reproduction of *B. tectorum* is physiologically limited in relatively warm and dry salt desert sites at lower elevations by frequent, low precipitation years, constrained by low soil temperatures in mountain big sagebrush sites at high elevations, and optimal under relatively moderate temperature and water

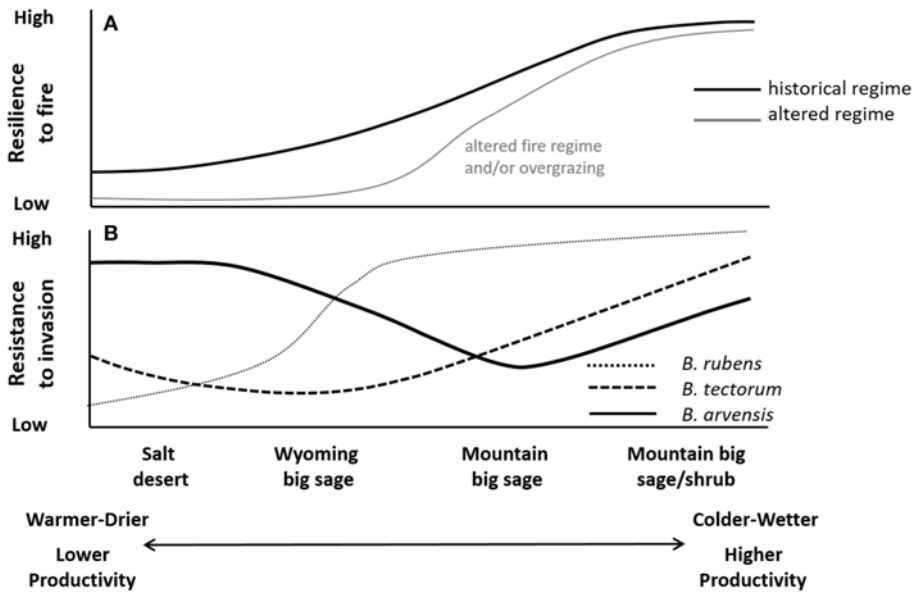

FIGURE 7 | Hypothetical **(A)** resilience to historical and altered disturbance regimes (primary altered regime characteristic labeled in gray) and **(B)** resistance to common invasive annual grass species in the Cold Deserts. Adapted from Chambers et al. (2014a).

availability in Wyoming big sagebrush sites at mid elevations (Meyer et al., 2001; Chambers et al., 2007). In contrast, *B rubens* (red brome) is less cold tolerant (Bykova and Sage, 2012) and occurs primarily on warm and dry salt desert sites and Warm/Cold-desert transitional sites (Salo, 2005). Field brome (*B. arvensis*) is limited on warm and dry as well as cold sites, but can be relatively abundant on cool and moist sites (Baskin and Baskin, 1981). In the Wyoming basin and Colorado Plateau, where summer precipitation (ustic soil moisture regimes) and the relative abundance of perennial grasses is higher, invasive annual grasses appear less competitive (**Figure 5**) (Bradley, 2009; Bradley et al., 2018). None-the-less, these invasive grasses can persist following disturbance and are a rapidly emerging problem (Bradford and Lauenroth, 2006; Mealor et al., 2013) that may be further affected by climate change (Bradley et al., 2016). Other invasive annual grasses, such as medusahead (*Taeniatherum caput-medusae*) and North Africa grass (*Ventenata dubia*) are well-established in the Cold Deserts and appear to be expanding (Wallace et al., 2015), but their climatic tolerances are less well-studied.

Resistance in Cold Deserts is decreased by disturbances and stressors that increase dispersal, reduce perennial species cover and abundance, and elevate resource availability. The probability of *B. tectorum* presence is elevated significantly adjacent to agriculture, power lines, and roads (Bradley, 2010). *Bromus tectorum* presence is strongly associated with decreases in perennial native species, especially grasses and forbs, biological soil crusts, and distance between perennial herbaceous species (gaps) due to improper livestock grazing across a range of vegetation types Dettweiler-Robinson et al., 2013; Reisner et al., 2013.

Potential for development of invasive grass-fire cycles

The potential for invasive grass-fire cycles to develop is greatest in areas with low to moderate resilience to fire and resistance to invasive annual grasses. In fuel-limited salt desert and Wyoming big sagebrush types, invasion of non-native annual grasses and forbs can alter plant functional group composition within vegetation types and increase the amount and availability of fuels following high precipitation years (Littell et al., 2009; Abatzoglou and Kolden, 2013). Even small amounts of *B. tectorum* cover are associated with large increases in wildfire probability; *B. tectorum* has advanced the time of wildfire by 10 days in summer and increased the chances of ignition by humans (Bradley et al., 2018). Although abundance of these species is generally low in the Wyoming Basin and Colorado Plateau, abundance increases with wildfire (Knight et al., 2014), particularly in drier areas Floyd et al., 2006; Shinneman and Baker, 2009.

Warm Deserts

General description

Warm Deserts are the hottest and driest regions of the western United States. Soil temperature regimes are either hot or very hot (hyperthermic; >22°C) and soil moisture is mostly aridic, meaning that the soil is dry for at least half of the growing season and moist for <90 consecutive days (Brooks et al., 2016). There is a significant gradient in seasonality of precipitation, where a mix of summer and winter precipitation characterizes the northern and western areas and predominantly summer precipitation characterizes the southern and eastern areas. As a result, the Chihuahuan Deserts are characterized by shrublands and grasslands that can support relatively high perennial plant cover (20–30%), while

the Mojave and Sonoran Deserts largely support shrublands where perennial cover of the most arid regions can be quite low (<7%). These differences are illustrated here for the Mojave Desert (**Figure 8**).

Resilience to fire

High elevation and desert montane vegetation such as sagebrush steppe, interior (Arizona) chaparral, and pinyon-juniper woodlands of the Mojave and Sonoran Deserts have higher resilience due to more frequent fires historically and fire tolerant plant functional groups (Brooks et al., 2018) (e.g., **Figure 8**). Desert grasslands of the Sonoran and Chihuahuan deserts, and riparian vegetation throughout the Warm Deserts, also have fire tolerant plant functional groups and thus relatively high resilience. In contrast, vegetation types typical of hotter and/or drier conditions, such as creosote bush scrub and saltbush scrub, had fewer fires historically and have low resilience to fire.

Resistance to invasion

Bromus rubens is the most ubiquitous invasive annual grass across the Warm Desert region (Brooks et al., 2016). It occurs in all but the hottest and driest regions, and is most abundant in middle elevation creosote bush scrub and blackbrush shrubland, especially in moister microsites beneath shrubs, in rock crevices, and on north-facing slopes (Brooks and Berry, 2006; Brooks, 2009; Klinger et al., 2011). *Schismus* spp. (Mediterranean split-grass) is widespread at lower elevations where it can dominate in interspaces and areas beneath shrub canopies (Brooks, 2009). *Bromus tectorum* is much more restricted in its geographic distribution and is typically most abundant at higher elevations (Klinger et al., 2011). Localized areas of higher soil moisture, such as roadsides, riparian areas, and agricultural/urban areas can support high levels of both *B. tectorum* and *B. diandrus* (ripgut brome) (Brooks, 2009; Dudley, 2009).

Perennial invasive grasses are becoming increasingly prevalent, especially in the monsoonal regions of the Sonoran Desert. This region has higher minimum temperatures and summer rainfall which promote establishment and growth of *P. ciliare*, especially in shrublands (Marshal et al., 2012). *Eragrostis lehmanniana* (Lehmann lovegrass) is a perennial grass introduced for forage that is highly invasive and can dominate desert grasslands (Van Devender et al., 1997). *Penniseum setaceum* (purple fountaingrass) is a perennial grass introduced through ornamental horticulture that is currently expanding its range near urban areas in the Mojave Desert (Brooks, 2009).

Resistance to invasive grassed decreases along road corridors and near urban areas with high propagule pressure (Brooks, 2009) and where current or historic livestock grazing has reduced perennial vegetation cover (Brooks and Pyke, 2001; Brooks et al., 2007). Long-term reductions in resistance to invasion can be caused by repeated fires at higher elevations, or even single fires at lower elevations (Klinger and Brooks, 2017). Also, atmospheric nitrogen deposition downwind of urban or agricultural areas can increase soil nitrogen availability and biomass of invasive annual grasses and may elevate the potential for fire, and invasive grass dominance (Brooks, 2003; Allen et al., 2009; Rao and Allen, 2010; Rao et al., 2014).

Potential for a grass-fire cycle

In Mojave and Sonoran Deserts shrublands susceptibility to grass-fire cycles is greater where: (1) climatic regimes support native vegetation, which is not quite sufficient in amount, continuity, or flammability to have promoted periodic historical fires and thus to have evolved fire-tolerant traits; and (2) seasonal precipitation is sufficient to allow invasive annual

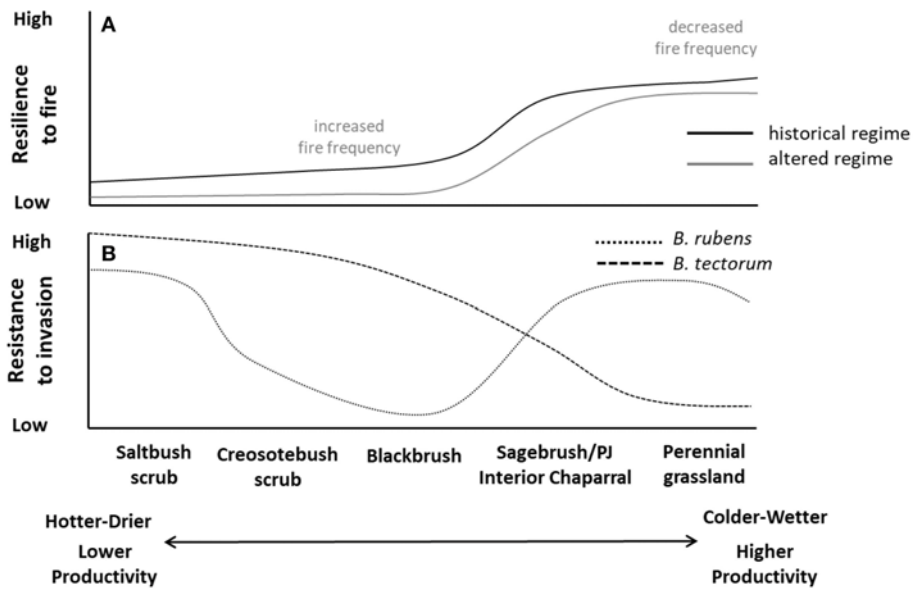

FIGURE 8 | Hypothetical **(A)** resilience to historical and altered fire regimes (primary altered regime characteristic labeled in gray) and **(B)** resistance to common invasive annual grass species in the Mojave Desert. Adapted from Brooks et al. (2016).

grasses to establish, spread, and eventually dominate landscapes. For example, blackbrush scrub has insufficient fuels to carry fire under most conditions and exhibits slow recovery following fire, so resilience to fire tends to be low. High rainfall years can increase fine fuels from *B. tectorum and B. rubens* and result in large stand replacing fires, very slow recovery of native perennial shrubs, and rapid increases in *Bromus* spp. that ultimately cause reduced fire return intervals, extirpation of the dominant shrub species over large areas, and progressive dominance of the invasive annual grasses (Brooks et al., 2018; Klinger et al., 2018).

In grasslands of the eastern Sonoran and Chihuahuan Deserts, conditions that reduce the vigor of native perennial grasses (e.g., drought or excessive livestock grazing) can reduce resistance to invasive perennial grasses (Olsson et al., 2012). Some species, such *E. lehmanniana*, have differing phenology than the native perennial grasses and are shifting fire seasons in ways that negatively affect native species.

Mediterranean Ecoregion

General description

The Mediterranean region of California has relatively cool and wet winters and hot and dry summers (Keeley and Syphard, 2018). Soil temperature regimes are mostly hot (thermic) to warm (mesic) and moisture regimes are mostly dry (aridic) to winter moist (xeric). Compared to the Cold Deserts, the Mediterranean region has warmer temperatures; compared to the Warm Deserts, it has similar temperatures but moister conditions and receives a much higher percentage of precipitation in winter (Brooks et al., 2016). A strong productivity gradient exists where sage scrub is at the hotter and drier end and mixed conifer forest is at the cooler and wetter end (**Figure 9**). Perennial grasslands, oak savannas and woodlands, and chaparral occupy the middle of the gradient.

Resilience to fire

Resilience to fire is lower in hotter and drier areas and higher in cooler and wetter areas (**Figure 9**) (Keeley and Syphard, 2018). Only relict stands of saltbush scrub remain due to conversion to agriculture, low resistance to invasive annual grasses, and low resilience to fire (Wills, 2018). Sage scrub is still abundant where conditions are more mesic and constituent species are more fire tolerant, but it is less abundant in more arid areas where the constituent species are less fire tolerant (Borchert and Davis, 2018; Keeley and Syphard, 2018). Forest, woodlands, shrublands, and grasslands of the central coast are most resilient to fire due to the climatically moderating influences of the Pacific Ocean and a history of periodic fire (Borchert and Davis, 2018). Chaparral is highly resilient to fire, except under very short fire return intervals driven by annual grass invasions (Keeley and Syphard, 2018).

Resistance to invasion

The Mediterranean region has a long history of plant invasions dating to the mid-1700s and the Spanish missionary period (Heady, 1977). Many of the annual invasive grasses, like *B. rubens*, were originally introduced as seed contaminants in wheat and barley (Salo, 2005). Land use changes associated with human settlement, including widespread tilling associated with agriculture and extensive livestock grazing, reduced resistance of native ecosystems to invasion and resulted in spread of the invaders (Keeley and Syphard, 2018). Annual grasses in the genera *Bromus* and *Avena* are especially prevalent in Mediterranean regions (Klinger et al., 2011, 2018; Brooks et al.,

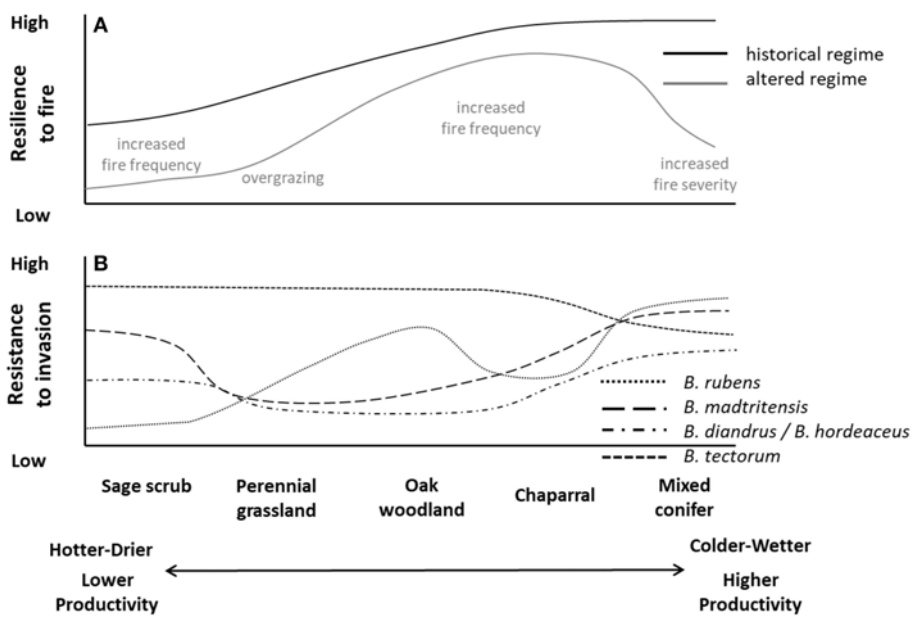

FIGURE 9 | Hypothetical **(A)** resilience to historical and altered fire regimes (primary altered regime characteristic labeled in gray) and **(B)** resistance to common invasive annual grass species in the Mediterranean California ecoregion. Adapted from Brooks et al. (2016).

2016). Invasion of perennial grass species, such as *Cortaderia* spp. (jubatagrass, pampasgrass), into wildland areas is facilitated by intentional introductions for ornamental horticulture (California Invasive Plant Council [Cal-IPC], 2018). High cover of native perennial species in chaparral tends to increase resistance to invasion, although fire can provide windows of lower resistance to invasion. Annual non-native forbs with potential to promote fires (e.g., *Brassica* spp.) are also abundant in these systems and typically have long-lived seedbanks that can persist for decades and then germinate following fire.

Potential for a grass-fire cycle

Two interrelated mechanisms can lead to grass-fire cycles in Mediterranean shrublands and reduce native shrubland resilience to fire and resistance to invasive grasses. Fire return intervals shifting from 20 to 50 years to 1–15 years can cause mortality of shrub seedlings and resprouting adults and significantly delay native shrub recovery (Keeley and Syphard, 2018). Also increased urbanization and conversion to agriculture can fragment shrubland patches, provide propagule sources for new invaders, and increase atmospheric nitrogen deposition—conditions that can increase fine fuels and fire frequency (Klinger et al., 2018). Grass-fire cycles have the highest potential to occur in more arid vegetation types such as saltbush scrub of the Central Valley and sage scrub of the interior valleys of southern California. Although the understory of oak savannas is now dominated by non-native annuals (>90% in many cases), these species have replaced mostly native herbaceous annuals with somewhat similar fuel characteristics and thus may not substantively change the fire regime.

USING A MULTI-SCALE, RESILIENCE-BASED FRAMEWORK TO MANAGE INVASIVE GRASS-FIRE CYCLES

The extent of grass invasions and development of invasive grass-fire cycles around the globe indicate the need for strategic, multi-scale approaches that enable managers to determine where and how to invest limited fire management and restoration resources. An understanding of ecological resilience to disturbances like wildfire and resistance to invasive grasses can be used to facilitate regional planning and prioritize management actions such as fuels management, early detection and rapid response to new invasions (U. S. Department of the Interior [USDOI], 2016), fire suppression, and passive or active restoration (Chambers et al., 2014a, 2017a,b). Here, we provide information to apply the multi-scale, resilience-based framework described in[1] to address invasive grass-fire cycles in arid and semiarid shrublands and woodlands.

The framework for prioritizing management actions to address invasive grass-fire cycles at landscape scales is based on (1) general resilience as indicated by environmental characteristics and ecosystem attributes and processes, (2) spatial resilience based on landscape composition and configuration, and thus capacity to support high value resources, and (3) interactions of general and spatial resilience with invasive annual grasses and fire. In the framework, a spatially explicit approach is used that enables managers to quantify and visualize differences in general and spatial resilience across the landscape in relation to cover of invasive annuals and fire risk. Assessments are typically conducted at the scale of one or more Level III ecoregions (**Figure 4**), and funding and human resources are allocated in a manner designed to maximize management investments. Here, we provide an example of how to use this framework for the Cold Deserts.

Steps in the Process

Develop the Management Objectives

Identifying appropriate management objectives and strategies in the context of long-term adaptive management programs is critical for long-term success. Adaptive management programs are designed to reduce uncertainty in the effectiveness of management actions by continually evaluating and adjusting management objectives and strategies to improve the effectiveness of management actions overtime. Adaptive management programs facilitate "learning by doing" and can help land managers and stakeholders examine the context, options, and probable outcomes of decisions through an explicit and repeatable process (Allen et al., 2011; Marcot et al., 2012; Thompson et al., 2013).

- Objectives for addressing invasive grass-fire cycles provide the basis for managing ecosystems to increase their capacity to reorganize and adjust to ongoing change while providing necessary ecosystem services. Key management objectives for the Cold Deserts typically include:
- Strategic location of firefighting resources to suppress wildfires in areas with high to very high fire risk and high value resources and habitats in intact salt desert and Wyoming big sagebrush types, and to prevent invasive grass fueled fires from burning through areas with high value resources and habitats in general;
- Prioritization of fuel treatments, specifically where, how much, and how to treat surface and canopy fuel to prevent uncharacteristic wildfires and protect high value resources and habitat;
- Prioritization of areas with little to no invasive plants for early detection and rapid response weed management strategies (U. S. Department of the Interior [USDOI], 2016), low to moderate levels of invasion for active weed management/restoration, and high levels of invasion for containment (Mealor et al., 2013);
- Prioritization of post-fire restoration treatments (soil stabilization, weed control, seeding) to focus on areas that will benefit most, specifically those areas that require soil surface stabilization or lack sufficient perennial natives to recover without treatments but still have the capacity to recover to a desirable state.

Develop Landscape Indicators of General Resilience and Resistance to Invasive Grasses

Information on the general resilience of ecosystems enables managers to: (1) evaluate differences in ecosystem responses

to disturbance and recovery potentials across landscapes; (2) identify locations where ecosystems may exhibit critical transitions to novel alternative states in response to fire or other drivers; and (3) determine where conservation and restoration investments will have the greatest benefits[1]. Environmental characteristics (**Table 2**) are commonly used as indicators of general resilience and resistance to invasive plants because of their effects on ecosystem attributes and processes and plant invasions. In arid and semi-arid shrublands and woodlands, soil temperature and moisture regimes provide one of the most complete data sets for understanding and mapping potential resilience and resistance to invasive annual grasses. Soil temperature and moisture regimes are mapped for most of the region and are available through the USDA Natural Resources Conservation Service, Web Soil Survey (**Figure 10A**) (https://websoilsurvey.nrcs.usda.gov). In the Cold Deserts, the dominant vegetation (ecological) types have been characterized according to soil temperature and moisture regimes, general resilience to disturbance, and resistance to invasive annual grasses (Chambers et al., 2017a) based on recent research (Chambers et al., 2007, 2014b, 2017b; Condon et al., 2011; Davies et al., 2012; Urza et al., 2017) and expert input. State-and-transition models, which provide information on the alternative states, ranges of variability within states, and processes that cause plant community shifts within states as well as transitions among states, have been developed for the dominant vegetation types (Chambers et al., 2017a). To facilitate landscape analyses and prioritization, soil temperature and moisture regime subclasses have been used to categorize relative resilience to disturbance and resistance to invasive annual grasses as high, moderate, or low across the Cold Deserts (**Figure 10B**) (Maestas et al., 2016; Chambers et al., 2017a).

Develop an Understanding of Spatial Resilience

A understanding of spatial resilience in the context of landscapes provides the necessary information for creating functionally connected networks that provide ecosystem services and conserve resources and species. The landscape context provides information on (1) availability of resources and habitats to support species populations, (2) connectivity among resources and habitats, and (3) spatial constraints on ecological resilience and system recovery potential (Holl and Aide, 2011; Rudnick

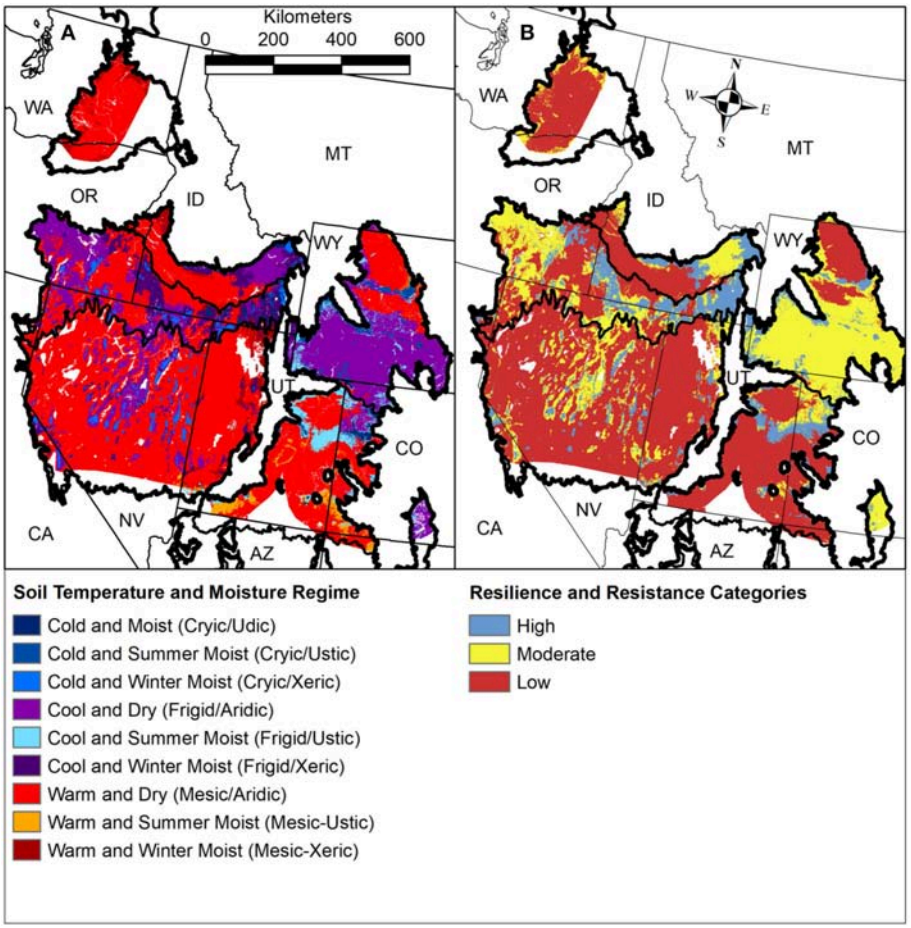

FIGURE 10 | (A) Soil temperature and moisture regimes by moisture subclass derived from the Web Soil Survey for the Cold Deserts in western North America and **(B)** resilience and resistance categories developed from the soil temperature and moisture regimes (Maestas et al., 2016; Chambers et al., 2017a).

et al., 2012; McIntyre et al., 2014; Rappaport et al., 2015; Ricca et al., 2018). In the Cold Deserts, sagebrush ecosystems and the species that depend on them are threatened by progressive expansion of invasive annual grasses and development of grass-fire cycles and are a high priority for management (Knick et al., 2011; Miller et al., 2011; Davies et al., 2012). Landscape cover of sagebrush provides a regional metric of habitat availability and has been shown to be an important predictor of persistence of sagebrush obligate species (Rowland et al., 2006; Aldridge et al., 2008; Hanser et al., 2011; Wisdom et al., 2011; Knick et al., 2013).

Sage-grouse are broadly distributed species that occupy a diversity of environments containing sagebrush and have been managed as umbrella species for over 350 species of plants and animals that depend on sagebrush ecosystems (Suring et al., 2005; Knick et al., 2013).

Greater sage-grouse has been considered for listing under the U.S. Endangered Species Act several times and its status will be reevaluated in 2020 (U.S. Department of the Interior, Fish and Wildlife Service [USFWS], 2015). Here we use ecological minimum requirements underlying sage-grouse distributions (Knick et al., 2013; Chambers et al., 2014c) as a metric for evaluating spatial resilience in sagebrush ecosystems. Sagebrush landscape cover is derived from remotely sensed land cover data using a moving window analysis (Knick et al., 2013). Prior analyses show that percentage landscape cover of sagebrush around Greater sage-grouse leks (mating sites) is an indicator of the relative probability of lek persistence in different areas within the sagebrush biome (Aldridge et al., 2008; Wisdom et al., 2011; Knick et al., 2013). Greater sage-grouse lek persistence is low with 1 to 25% landscape cover of sagebrush, intermediate with 25 to 65%, and high with >65% (Chambers et al., 2014c). Although metrics more specific to sage-grouse have been developed, such as the probability of breeding bird habitat (Doherty et al., 2016), we use a modification of the three categories of landscape cover of sagebrush as a general metric of spatial resilience (**Figure 11A**). Intersecting the resilience and resistance index with the landscape cover of sagebrush categories provides information on sagebrush habitat availability and connectivity, potential for recovery following wildfire, and spatial constraints on recovery (**Figure 11B**).

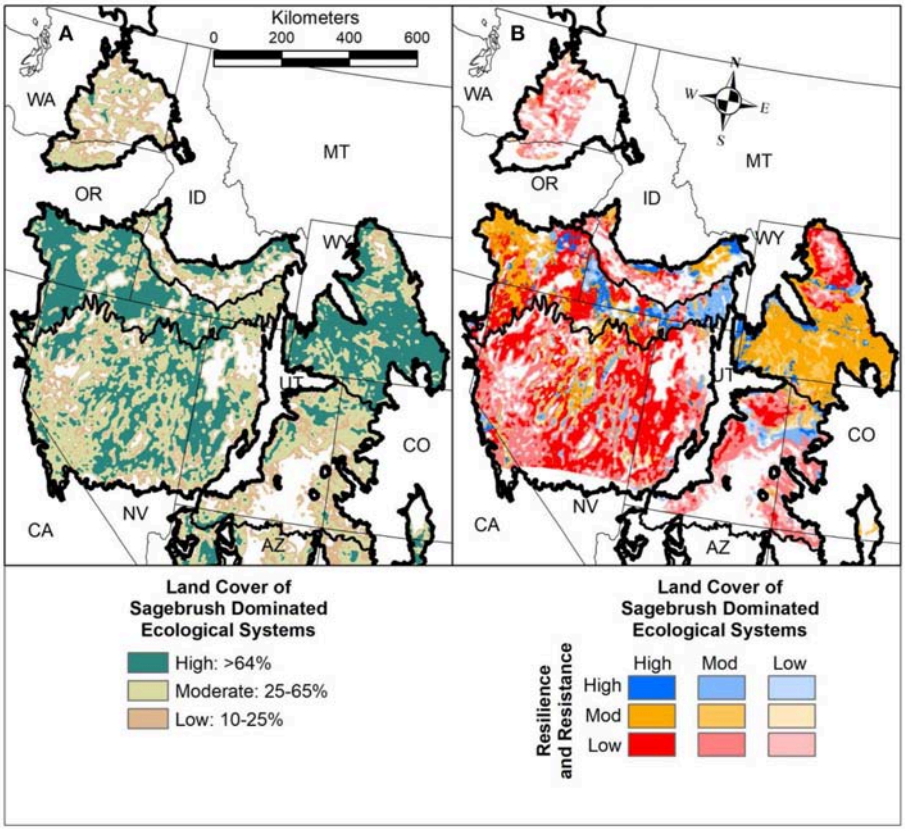

FIGURE 11 | (A) Landscape cover of sagebrush in the Cold Deserts of western North America (low = 10–25%, moderate = 25–65%, high = >65%) (U.S. Department of the Interior, 2014). Categories of sagebrush landscape cover are based on ecological minimum requirements underlying sage-grouse distributions (Knick et al., 2013; Chambers et al., 2014c). Percentage of sagebrush within each of the categories was determined within a 5 km radius of each sagebrush pixel. **(B)** Landscape cover of sagebrush categories intersected with resilience and resistance categories developed from soil temperature and moisture regimes (Maestas et al., 2016; Chambers et al., 2017a).

Develop an Understanding of Fire Risk in Relation to Grass Invasions

Identifying fire risk in relation to grass invasions facilitates prioritization and selection of effective management strategies. Information on the probability of wildfire and land cover of invasive plants enables managers to: (1) identify vegetation types and areas on the landscape with the potential for transitions to less-desirable alternative states; (2) target management actions designed to reduce or mitigate wildfire and invasion; and (3) facilitate transformation to new states where disturbances and/or climate change are preventing return to desirable prior states. A large-fire risk assessment for the United States has been developed from modeled burn probabilities and fire size distributions based on weather data, spatial data on fuel structure and topography, historical fire data, and fire suppression effects (Finney et al., 2011), which was recently updated (Short et al., 2016). Also, cover estimates of annual forbs and grasses in the western United States were recently derived by combining over 30,000 vegetation field plots with satellite imagery, gridded meteorology, and abiotic land surface data (**Figure 6**) (Jones et al., 2018). Intersecting the resilience and resistance index, sagebrush landscape cover categories, and large fire risk provides spatially explicit information not only on the likelihood of large fires, but also on likely responses to those fires and effects on high value habitat (**Figure 12A**). Intersecting the resilience and resistance index, sagebrush landscape cover categories, and percentage land cover of annual forbs and grasses provides spatially explicit information on the current magnitude of invasion and thus the types of management actions most likely to be needed and effective, both pre- and post-fire (**Figure 12B**). These maps can be scaled down to local field offices or project areas to facilitate planning designed

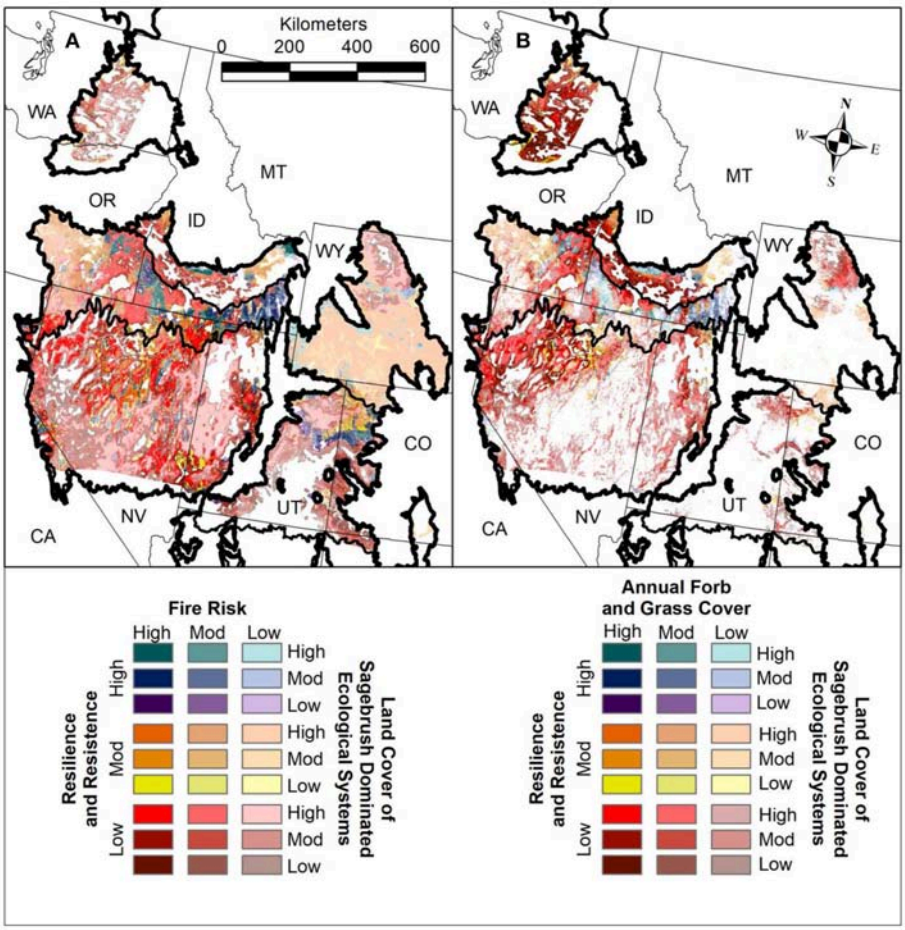

FIGURE 12 | (A) Map illustrating relative fire risk for sagebrush dominated ecosystems in the Cold Deserts. Large fire risk (U.S. Department of Agriculture, Forest Service [USDA FS], 2018) is intersected with resilience and resistance categories developed from soil temperature and moisture regimes (Maestas et al., 2016; Chambers et al., 2017a), and landscape cover of sagebrush categories (low = <25%, moderate = 25–65%, high = >65%) based on ecological minimum requirements underlying sage-grouse distributions (Knick et al., 2013; Chambers et al., 2014c). **(B)** Map of annual forb and grass risk for sagebrush dominated ecosystems in the Cold Deserts. Continuous land cover of annual forbs and grasses (low = 10–20%; moderate = 20–40%; high = >40%) (Jones et al., 2018) is intersected with resilience and resistance categories developed from soil temperature and moisture regimes (Maestas et al., 2016; Chambers et al., 2017a) and landscape cover of sagebrush categories based on ecological minimum requirements underlying sage-grouse distributions (Knick et al., 2013; Chambers et al., 2014c).

TABLE 3 | Decision matrix for prioritizing areas for conservation and restoration investments and determining appropriate management strategies based on resilience concepts (Chambers et al., 2014a, 2017a)[1].

Resilience & Resistance of Sagebrush Ecosystem	Proportion of Landscape Dominated by Sagebrush: *Low* = 10- 25%	*Moderate* = 25-65%	*High* = > 65%
High	**RESTORATION/RECOVERY POTENTIAL HIGH** *Native grasses and forbs often sufficient for recovery after disturbance* *Risk of annual invasive grasses becoming dominant is low* *Seeding/transplanting success typically high*		
	Longer timeframe for recovery may require moderate intervention	Some intervention to enhance connectivity and improve function	Minimal intervention; preventative management to maintain function
Moderate	**RESTORATION/RECOVERY POTENTIAL VARIABLE** *Native grasses and forbs often adequate for recovery after disturbance* *Risk of annual invasive grasses becoming dominant is moderate* *Seeding/transplanting success depends on site characteristics*		
	Longer timeframe for recovery likely requires moderate-to-high intervention	Moderate intervention to minimize invasive risks, enhance connectivity, and improve function	Some intervention needed to minimize risk of invasion; preventative management to maintain function
Low	**RESTORATION/RECOVERY POTENTIAL LOW** *Native grasses and forbs often inadequate for recovery after disturbance* *Risk of annual invasive grasses becoming dominant is high* *Seeding/transplanting may require multiple interventions*		
	Recovery unlikely without significant intervention over long timeframe	High intervention to minimize invasive risks, enhance connectivity, and improve function	Moderate-to-high amount of intervention to minimize risk of invasion and maintain and enhance function

Rows show relative resilience to disturbance and resistance to invasive annual grasses (high, moderate, low). Resilience and resistance categories were derived from soil temperature and moisture regimes (Maestas et al., 2016; Chambers et al., 2017a) and relate to broad-scale sagebrush ecological types. Columns show the landscape cover of sagebrush (low = <0.25%, moderate =25–65%, high = >65%). Categories of sagebrush landscape cover are based on ecological minimum requirements underlying sage-grouse distributions (Knick et al., 2013; Chambers et al., 2014c) and are used here as a metric for evaluating spatial resilience. Considerations for using the matrix and determining management strategies are in text.

to locate management strategies where they will be most effective (**Figure 13**).

Areas with high to very high risk of large fires and high cover of annual grasses and forbs are typically locations where annual grass-fire cycles have developed (**Figures 12A,B**). These areas occur in the western part of the region with predominantly winter precipitation (**Figure 5**). In the western part of the region, many areas with low resilience and resistance and high landscape cover of sagebrush have high to very high risk of large fires and high cover of annual forbs and grasses (**Figures 12A,B**). In moderate and especially high resilience areas, the cover of annual forbs and grasses is generally lower. However, fire risk is not affected by resilience category and areas with both low and high resilience have high to very high fire risk. In the eastern part of the region, both large fire risk and cover of annual grasses and forbs is lower (**Figures 12A,B**). However, areas with moderate fire risk and moderate cover of annual grasses and forbs exist in areas with high landscape cover of sagebrush.

Management Applications

The resilience and resistance matrix is a decision-tool that provides the ability to consider resilience to wildfire and resistance to invasive grasses along with spatial resilience when prioritizing areas for management actions to prevent development of invasive grass-fire cycles at landscape scales (**Table 3**). The matrix allows managers to determine both the locations where management actions are likely to have the greatest benefits and the types of activities most likely to be effective. In the matrix, as resilience and resistance go from low to high (indicated by the lower to upper rows), the recovery potential increases as a function of the amount of change from the initial or desired state and the recovery time following disturbance. As landscape cover of sagebrush, a surrogate for spatial resilience, goes from low to high within these same systems (indicated by the columns), the capacity to support high value habitat and resources increases as a function of the size and shape of habitat and resource patches and their connectivity. Geospatial analyses and maps of landscape cover of sagebrush and relative resilience and resistance coupled with the risk of large fires and cover of annual forbs and grasses informs both management priorities and strategies within planning areas (**Figure 13**).

The relative resilience to wildfire and resistance to invasive grasses strongly influences the response of an area to management strategies aimed at preventing or minimizing invasion and spread of non-native grasses and development of invasive grass-fire cycles (Chambers et al., 2014a,b, 2017a,c). Areas with high resilience and resistance often have the capacity to return to the prior or desired state with minimal investment following disturbances such as wildfire, while those with moderate resilience and resistance depend on both environment conditions and ecosystem attributes and require more detailed assessments to determine the most effective management strategies. Areas with low resilience and resistance are often among the most difficult to improve or restore and multiple management interventions may be required to obtain the desired state. In those areas where climate change effects are projected to be severe, management actions may need to help ecosystems transition to new climatic regimes (e.g., Millar et al., 2007; Halofsky et al., 2018a,b; Snyder et al., 2018).

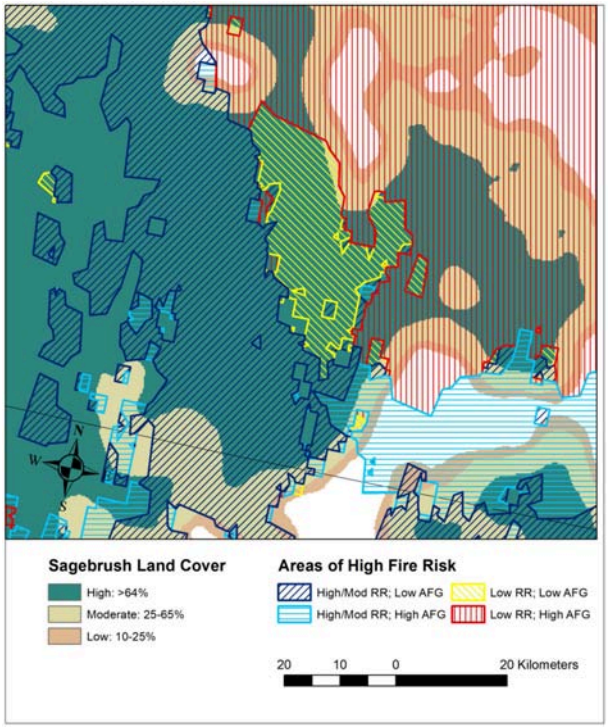

FIGURE 13 | A map of an area on the Idaho/Nevada border that overlays relative sagebrush dominance with areas of high to very high fire risk that have (1) high to moderate resilience and resistance and low annual forb and grass cover, (2) high to moderate resilience and resistance and high annual forb and grass cover, (3) low resilience and resistance and low annual forb and grass cover, and (4) low resilience and resistance and high annual forb and grass cover. The geospatial data sources are described in **Figure 12**. Areas with high cover of sagebrush that have low resilience and resistance, high fire risk, and low cover of annual forbs and grasses are among the highest priorities for protective management strategies, such as conservation easements and early detection and rapid response management of invasive plants. Areas with moderate cover of sagebrush that have high to very high fire risk are areas to consider for treatments that will increase connectivity and resilience to wildfire, such as fuel treatments, fuel breaks, and seeding after wildfires. Areas with low cover of sagebrush may have limited ability to support desired resources and habitats and where associated with high levels of invasion or human development, fire prevention, preparedness, and suppression may be high priorities.

The spatial resilience of an area is influenced by (1) resilience to disturbance and resistance to invasive grasses, which influence recovery potentials and the propensity to change states, and (2) anthropogenic developments, which fragment habitats, result in introductions of novel species, and can preclude return to prior states. An area with high landscape cover of sagebrush and high resilience to disturbance and resistance to invasive grasses may have relatively higher spatial resilience over time than one with low resilience to disturbance and resistance to invasive grasses. In contrast, an area with low landscape cover of sagebrush and high resilience to disturbance and resistance to invasive grasses may have similar spatial resilience to an area with low resilience

to disturbance and resistance to invasive grasses if anthropogenic development, such as agriculture or oil and gas wells, is causing the loss of spatial resilience.

Areas with high landscape cover of sagebrush are high priorities for protective management across resilience and resistance categories, because they are more likely to be comprised of functioning ecosystems with relatively intact habitat and resource patches (**Figures 12A,B**) (Chambers et al., 2014b, 2017a,b). Areas with low resilience and resistance, high landscape cover of sagebrush, and high fire risk are among the highest priorities for protective management, because they have the highest risk of developing invasive grass-fire cycles and of undesirable state changes (**Figure 13**). In general, protective management strategies to reduce the risk of non-native grass invasions and altered fire regimes include: (1) reducing land use and new development and establishing conservation easements to minimize invasion vectors and corridors and human-caused fire starts; (2) ensuring that land uses and land treatments maintain or increase perennial native grasses and forbs—the plant functional types that enable recovery and compete with invasive annuals post-fire; (3) implementing early detection and rapid response strategies in areas at high risk of invasion or spread of invaders, and in association with developments and transportation/utility corridors (California Invasive Plant Council [Cal-IPC], 2012; Mealor et al., 2013) (4) prepositioning firefighting resources in areas of high fire risk, and managing fires to maintain resources an habitats; (5) implementing fuel treatments, including fuel breaks, in a manner that maintains or increases connectivity and prevents new invasions; and (6) seeding natives adapted to local conditions and a wide range of climatic conditions during post-fire restoration in areas where insufficient native perennials exist for unassisted recovery (Chambers et al., 2017a).

Areas with moderate landscape cover of sagebrush are often priorities for improving ecosystem functioning, habitat connectivity, and thus spatial resilience (**Figures 12A,B**, **13**) (Chambers et al., 2014b, 2017a). Many of the same strategies apply as for areas with high landscape cover of sagebrush. Additional strategies may include: (1) implementing fuel treatments designed to increase connectivity and resilience to fire, such as removal of conifers expanding into sagebrush ecosystems; (2) thinning overly dense sagebrush stands and interseeding with perennial native grasses to improve habitat and increase resilience to fire (Huber-Sannwald and Pyke, 2005); (3) seeding or transplanting sagebrush and seeding a diverse mix of native species to reconnect intact habitats after wildfires (Pyke, 2011); and (4) managing livestock grazing and wild horse and burro numbers in a manner that increases treatment success. Consistent and repeated management interventions will likely be needed for these strategies to succeed in areas with low resilience and resistance, especially in areas with low to moderate cover of invasive forbs and grasses.

In areas with low landscape cover of sagebrush, the ability to increase spatial resilience and capacity to support desired resources and habitats may be limited by environmental factors, level of invasion, or amount of human development (**Figures 12A,B**, **13**). These areas typically require higher levels of intervention over longer-timeframes. Where associated with high levels of invasion or human development, fire prevention, preparedness, and suppression may be high priorities. These areas are often sources of invasive plants and vectors for their spread (Gelbard and Belnap, 2003; Bradley, 2010) and of human-caused fire ignitions (Fusco et al., 2016). Management strategies include: (1) reducing fuels and suppressing fires to protect both human developments and remaining habitat; (2) using integrated weed management strategies (California Invasive Plant Council [Cal-IPC], 2012; Mealor et al., 2013); (3) educating stakeholders and the public about the risk of weed invasions and invasive grass-fire cycles as well as the importance of natural resources and species habitats; and (4) implementing restoration/rehabilitation activities designed to reduce the spread of invasive plants and decrease fire risk.

n topographically diverse sagebrush landscapes, resilience to disturbance, resistance to invasion, and spatial resilience often varies not only across ecoregions but also across planning and project areas. To step landscape scale assessments and prioritizations down to local scales, it is necessary to evaluate the specific conditions that exist within the area, develop the appropriate objectives, and determine the best management strategies using the highest resolution geospatial data available. Planning areas occur over continuums of environmental conditions, such as effective precipitation, have differing land use histories and species compositions (Johnstone et al., 2016), and may be projected to experience different climate change effects. They also have different resource and habitat values and socio-economic concerns and constraints. Careful assessment of these factors and of past responses to both disturbances and management treatments helps ensure that management strategies are implemented in a manner that will maximize conservation and restoration investments. Rigorous monitoring of management outcomes related to clearly defined objectives provides the scientific basis for adjusting policies or management actions in response to dynamic conditions.

AUTHOR CONTRIBUTIONS

JC, MB, MG, and JM conceived the idea and developed the manuscript outline. JC led the writing of the manuscript. MB, MG, and JM contributed critically to the draft. DB, MJ, and BA contributed data and developed the map products. All authors gave final approval for publication.

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REVIEW
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Climate, Environment, and Disturbance History Govern Resilience of Western North American Forests

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Before the advent of intensive forest management and fire suppression, western North American forests exhibited a naturally occurring resistance and resilience to wildfires and other disturbances. Resilience, which encompasses resistance, reflects the amount of disruption an ecosystem can withstand before its structure or organization qualitatively shift to a different basin of attraction. In fire-maintained forests, resilience to disturbance events arose primarily from vegetation pattern-disturbance process interactions at several levels of organization. Using evidence from 15 ecoregions, spanning forests from Canada to Mexico, we review the properties of forests that reinforced qualities of resilience and resistance. We show examples of multi-level landscape resilience, of feedbacks within and among levels, and how conditions have changed under climatic and management influences. We highlight geographic similarities and important differences in the structure and organization of historical landscapes, their forest types, and in the conditions that have changed resilience and resistance to abrupt or large-scale

disruptions. We discuss the role of the regional climate in episodically or abruptly reorganizing plant and animal biogeography and forest resilience and resistance to disturbances. We give clear examples of these changes and suggest that managing for resilient forests is a construct that strongly depends on scale and human social values. It involves human communities actively working with the ecosystems they depend on, and the processes that shape them, to adapt landscapes, species, and human communities to climate change while maintaining core ecosystem processes and services. Finally, it compels us to embrace management approaches that incorporate ongoing disturbances and anticipated effects of climatic changes, and to support dynamically shifting patchworks of forest and non-forest. Doing so could make these shifting forest conditions and wildfire regimes less disruptive to individuals and society.

Keywords: resistance, meta-stability, climatic forcing, persistence, sustainability, self-organization, adaptive management

INTRODUCTION

The concepts of *resilience* and *resistance* broadly apply to ecological systems; they reflect the allied capacities of systems to *regain* and *retain* their fundamental structure, organization, and processes when impacted by stresses or disturbances (Holling, 1973). Resilient ecosystems are hierarchically organized (possessing unique structure and processes at several levels of organization) and adaptive (adjusting to environmental, climatic, and disturbance conditions; Angeler and Allen, 2016, and references therein). Conditions at each level of organization can exist in alternate states, or "basins of attraction" (**Figure 1**). Multi-level patterns, which fluctuate over space and time, emerge from periodic disturbances or stresses. Disturbances occur at predictable frequencies, within probable event-size distributions, and over a range of intensities that are unique to each level of organization; their frequency, size, and intensity depend upon the climatic and biophysical conditions at each level.

While helpful, this construct can miss interactive properties of resilience and resistance that are germane to landscapes exposed to wildfires, climate change, and humans. For example, Walker et al. (2004) portrayed resistance as a core component of resilience, where resilience depends on basin width (latitude-L), depth (resistance-R), proximity to the lip (precariousness-Pr), wall steepness, and panarchy–the strength of other impinging top-down and/or bottom-up influences (**Figure 1**). In a resilient system, it's unnecessary that any former position in a basin is regained, so long as the system remains in the basin. If the system is also resistant, it resides deep in the basin. Over time, resilient systems can share highly similar characteristics, but no two are identical. Instead, resilient systems tend to resonate within a cloud of conditions that define the latitude, depth, and shape of the basin (Scheffer et al., 2001). As resistance declines, so too does resilience. Without reestablishing durable resistance, future stresses likely result in system shifts to other basins of attraction (Tepley et al., 2018).

As global and regional temperatures and moisture deficits rise–leading to longer fire seasons and more pronounced seasonal drought–wildfire burned area is increasing in many Earth biomes, including those of western North America (Jolly et al., 2015; Abatzoglou and Williams, 2016). Highly altered fire frequency, severity, seasonality, and spatial extent can singly or collectively cause ecosystem change, particularly when coupled with climatic changes. Large patches ($>10^3$ ha) of high-severity [>75% of tree basal area [BA] or canopy cover [CC] killed] fires can catalyze changes in species distributions and community composition, because many plants are vulnerable during germination, establishment, and seedling life stages (Sprugel, 1991; Williams and Jackson, 2007). Combined with stresses imposed by human development and non-native species invasions, wildfires are testing the resilience and resistance of ecosystems worldwide (Holling, 1986; Davis et al., 2018; Stevens-Rumann et al., 2018). As climate and fire regimes change, new understanding is needed of both the inherent resilience of these novel ecosystems and of the implications to human communities and the ecosystem services they rely on.

In following sections, we examine the properties of dry, moist, cold, and boreal forests of the Western United States (US), Mexico (MX), and British Columbia (BC), Canada that make them resilient and resistant to wildfires and other stressors. We focus on drier forest ecoregions where fire and other disturbance agents are especially active. Fire is less frequent in moist to wet coastal forests of western North America, although research shows that wildfire and suppression of wildfire can affect ecosystem resilience in drier portions of the moist Douglas-fir/western hemlock forest type (Tepley et al., 2013). Despite border-crossing ecoregions and type similarities, forests of the US, Canada and Mexico are treated separately due to their distinct fire and forest management histories. We discuss the role of the ecoregional climate in episodically or abruptly reorganizing plant and animal biogeography or disturbance regimes (i.e., the frequency, severity, seasonality, and extent of disturbances). Using evidence from 15 Bailey ecoregions (Bailey, 1998, **Figure 2**) with varying forest types, we show clear examples of multi-level, historical forest landscape resilience; of cross-connections between levels; and change in resilient and resistant conditions under climatic and anthropogenic forcing. For example, aboriginal burning throughout western North

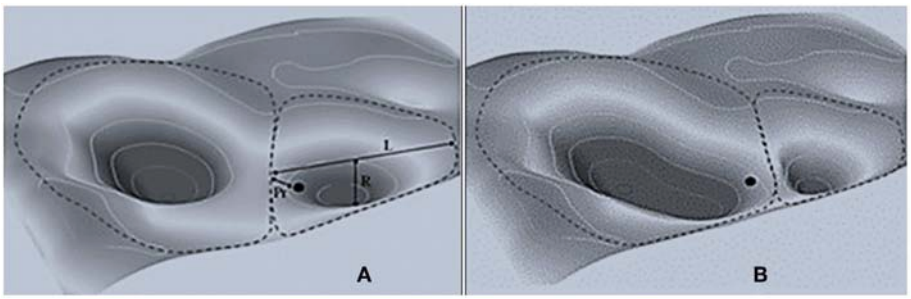

FIGURE 1 | Two landscapes (basins of attraction) and their constituent resilience attributes (from Walker et al., 2004 reprinted with permission). **(A)** A 3-D stability landscape showing two basins of attraction (dotted lines). In the smaller basin, the current position of the system (black dots) and three aspects of resilience, L, latitude (width of the basin), R, resistance (depth of the basin), and Pr, precariousness (proximity to the basin lip). **(B)** Changes in the broader landscape can result in contraction of the basin and expansion of an alternate basin. Without changing itself, the system has changed basins of attraction and is precariously positioned for additional changes.

America both buffered and amplified fire-climate interactions at patch to ecoregion levels (Taylor et al., 2016). Modern human populations can also increase an ecosystem's ignition frequency–changing its wildfire regime (Balch et al., 2017)—or human land uses can weaken or nullify climate influences on fire regimes (Syphard et al., 2017; Wahl et al., 2019).

We highlight geographic similarities and differences in the structure and organization of resilient landscapes, and in the conditions that alter resilience and resistance to abrupt or large-scale disruptions. We document similarities to reveal system-level properties that consistently emerge from broadly different physiographic domains, under the common influence of wildfires. Despite notable differences in regional geology, climate, and human interactions, we find fundamental properties guiding forest resilience and resistance across western North America. Multi-level pattern-process linkages exist between vegetation and disturbances, which co-adapt to changing environmental conditions and climate without altering their fundamental characteristics. Where these linkages are broken through abrupt changes in climatic forcing or by removing key disturbances from the landscape, vegetation dynamics can shift, and novel states or ecosystems can emerge, potentially compromising resilience to future disturbances.

THE CLIMATE OF WESTERN NORTH AMERICA–PAST, PRESENT, AND FUTURE

We begin our review by describing the influence of climate on fire regimes of western North American forests. Variability in regional climate strongly shapes forests and fire regimes, as well as any resilience or resistance they possess to stressors. Seasonal to annual temperature and precipitation are main drivers of forest productivity (**Figure 3**), which is often reflected in overstory and understory species composition, and overall forest structure (Stephenson, 1998). Productivity along with prior disturbance history determines the amount and characteristics of fuels, while seasonal variability in temperature and precipitation determine fuel moisture and availability to burn (**Figures 3B,C**). Thus, ecoregions can be described by distinctive space they inhabit along this productivity gradient, which runs from cool-wet to warm-dry climatic conditions (**Figure 3D**).

Among forest types of an ecoregion, wildfire regimes are typically climate-limited, where weather and atmospheric conditions are seldom sufficiently dry for combustion to occur, or fuel-limited, where frequent fires have consumed fuels or aridity limits abundance, or they are hybrid systems (**Figure 3D**, Agee, 1996; Krawchuk and Moritz, 2011). Fire regimes across this spectrum likewise vary, directly influencing the ways in which forests exhibit resilience and resistance to wildfires. At the moist end of the productivity gradient (**Figures 3C,D**), wildfire activity is *directly* climate-limited through occasional droughts that dry out naturally dense and typically moist vegetation (McKenzie and Littell, 2017). The wet forests of the coastal Pacific Northwest and western Cascade Mountains, cold subalpine, and some moist forests at moderate to high elevation or high latitude exemplify this scenario. Many summers, fire is limited by high fuel moisture or lack of ignitions; widespread burning is constrained to years with unusually severe drought. Under these more extreme conditions, high-severity fire effects may result in extensive tree mortality. Cold subalpine forests historically exhibited resilience to severe fires through tree species traits (e.g., cone serotiny, wind, bird, or mammal-dispersed seeds) and favorable climate that allowed for postfire regeneration; species composition and other properties returned to pre-fire conditions within decades to centuries (Baker, 2009). However, we note that even at the coldest and wettest end of this gradient there was variation in historical fire severity: fires burning under moderate fire weather generally exhibited more mixed-severity fire effects, including low- and moderate-severity patches (<25%, and 25–75% of tree BA or CC killed, respectively).

Fuel-limited ecosystems exist at the low end of the productivity gradient, where warm-dry climates contribute to area burned *indirectly* through their influence on woody fuel abundance and ignition frequency (Agee, 1996; Krawchuk and Moritz, 2011). While fuel moisture is often low and conducive to ignition, sparse understory vegetation and low tree density can limit surface fuels, fire spread, and flame lengths, making

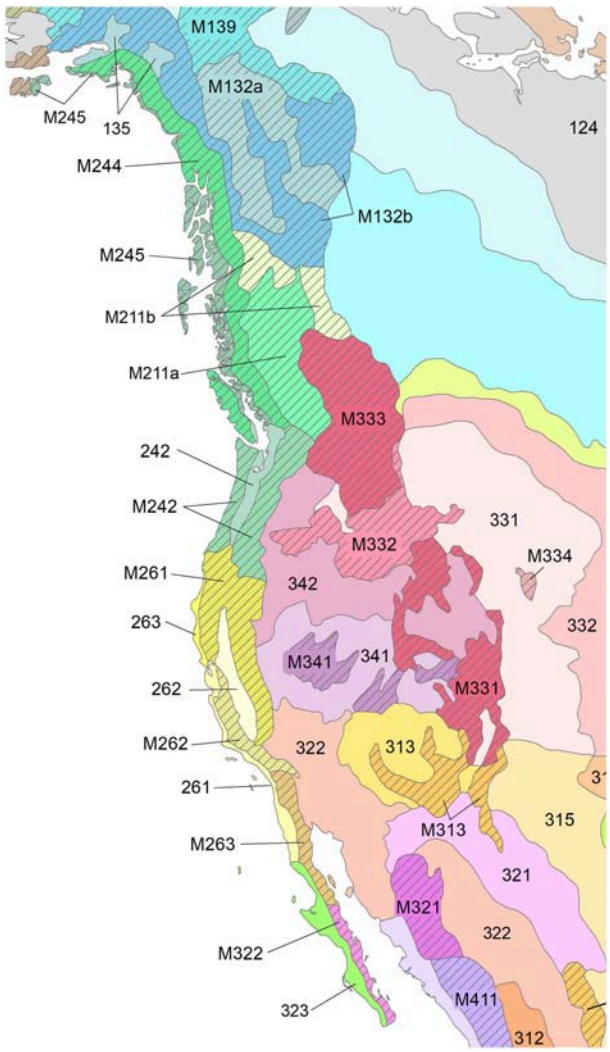

FIGURE 2 | Bailey provinces of western North America (Bailey, 1998). 135—Taiga—tundra, medium, M132a—Taiga—tundra, medium, M132b—Taiga—tundra, high, M139—Open woodland—tundra, M211a—Mixed forest—coniferous forest—tundra, medium, M211b—Mixed forest—coniferous forest—tundra, high, 242—Mixed forests, M242—Deciduous or mixed forest—coniferous forest—meadow, M244—Forest—meadow, high, M245—Forest—meadow, medium, 261—Dry steppe, 262—Mediterranean hard-leaved evergreen forests, open woodlands and shrub, 263—Redwood forests, M261—Mixed forest—coniferous forest—alpine meadow, M262—Mediterranean woodland or shrub—mixed or coniferous forest—steppe or meadow, M263—Shrub or woodland—steppe—meadow, 313—Coniferous open woodland and semideserts, 315—Shortgrass steppes, M313—Steppe or semidesert—mixed forest—alpine meadow or steppe, 321—Semideserts, M321—Semidesert—shrub—open woodland—steppe or alpine meadow, M322—Desert or semidesert—open woodland or shrub—desert or steppe, 331—Dry steppes, 332—Steppes, M331—Steppe—open woodland—coniferous forest—alpine meadow, M332—Steppe—coniferous forest—tundra, M333—Forest-steppe—coniferous forest—meadow—tundra, M334—Steppe—coniferous forest, 341—Semideserts and deserts, 342—Semideserts, M341—Semidesert—open woodland—coniferous forest—alpine meadow, M411—Open woodland—deciduous forest—coniferous forest—steppe or meadow. Reprinted with permission.

it difficult to initiate and spread crownfire. Another *indirect* influence of climate on fire activity occurs when above-average moisture availability promotes production of grass and herb cover, which facilitates widespread burning in subsequent years (Swetnam and Betancourt, 1998). Fires in fuel-limited systems typically burn with low- to moderate-severity, and due to a combination of fire behavior, species traits, and frequent woody fuel consumption, tree mortality can be low to moderate. Dry pine and mixed-conifer forests in lower elevations and at lower latitudes exemplify this scenario. Historically, thick-barked tree species (e.g., ponderosa pine-*Pinus ponderosa*, Jeffrey pine-*P. jeffreyi*, Douglas-fir-*Pseudotsuga menziesii*, and western larch-*Larix occidentalis*), and certain fire-adapted understory vegetation (e.g., bunchgrasses-*Festuca* spp., *Agropyron* spp., *Poa* spp., *Koelaria* spp., pinegrasses-*Calamagrostis* spp., buckbrush-*Ceanothus* spp., sagebrush-*Artemisia* spp., and bitterbrush-*Purshia* spp.) exhibited resistance to surface fires, surviving, or resprouting from roots or buried seeds in the weeks to years following fire.

Between this simplified dichotomy of climate- and fuel-limited are so-called "hybrid" systems (McKenzie and Littell, 2017), and they include a variety of mixed-conifer forests. Fires in these forests often burn with moderate-severity (Agee, 1996; Schoennagel et al., 2004; Hessburg et al., 2007), resulting in mixed surface and crownfire behavior and effects. Although simplified, this tripartite grouping is useful for understanding past and contemporary fire regimes, and how twenty-first-century climate change might impact fire regimes and forest resilience.

Climate has a strong influence on annual area burned. Robust correlations between seasonal to annual climate metrics and area burned (Higuera et al., 2015; Littell et al., 2018) implicate climate as the main driver of area burned. Tree-ring, lake-sediment, and paleoclimatic records from the more distant past highlight aspects of fire and forest resilience that provide important context for twenty-first-century change. For example, climate variability of the last millennium correlates well with area burned at interannual and centennial time scales. Years with large burned area are linked with warm-dry conditions (Schoennagel et al., 2005; Heyerdahl et al., 2008b; Williams et al., 2013), and area burned over decades to centuries broadly tracks variability in temperature and drought (Kitzberger et al., 2007; Marlon et al., 2012; Calder et al., 2015). In some cases, past periods of widespread burning associated with regional drought compromised forest resilience to wildfires, triggering shifts to non-forest, some of which persist today (Calder and Shuman, 2017). Documented shifts in the paleoclimatic record provide insights as to what we might expect under a warmer-drier climate.

Climate projections for western North America suggest that water deficits will increase over the twenty-first-century (Abatzoglou and Williams, 2016; McKenzie and Littell, 2017; Littell et al., 2018), with implications for future area burned and post-fire recovery of many forests (Davis et al., 2018, 2019). Expected outcomes vary across our tripartite grouping. For example, in cold and some moist forests, where fire has been

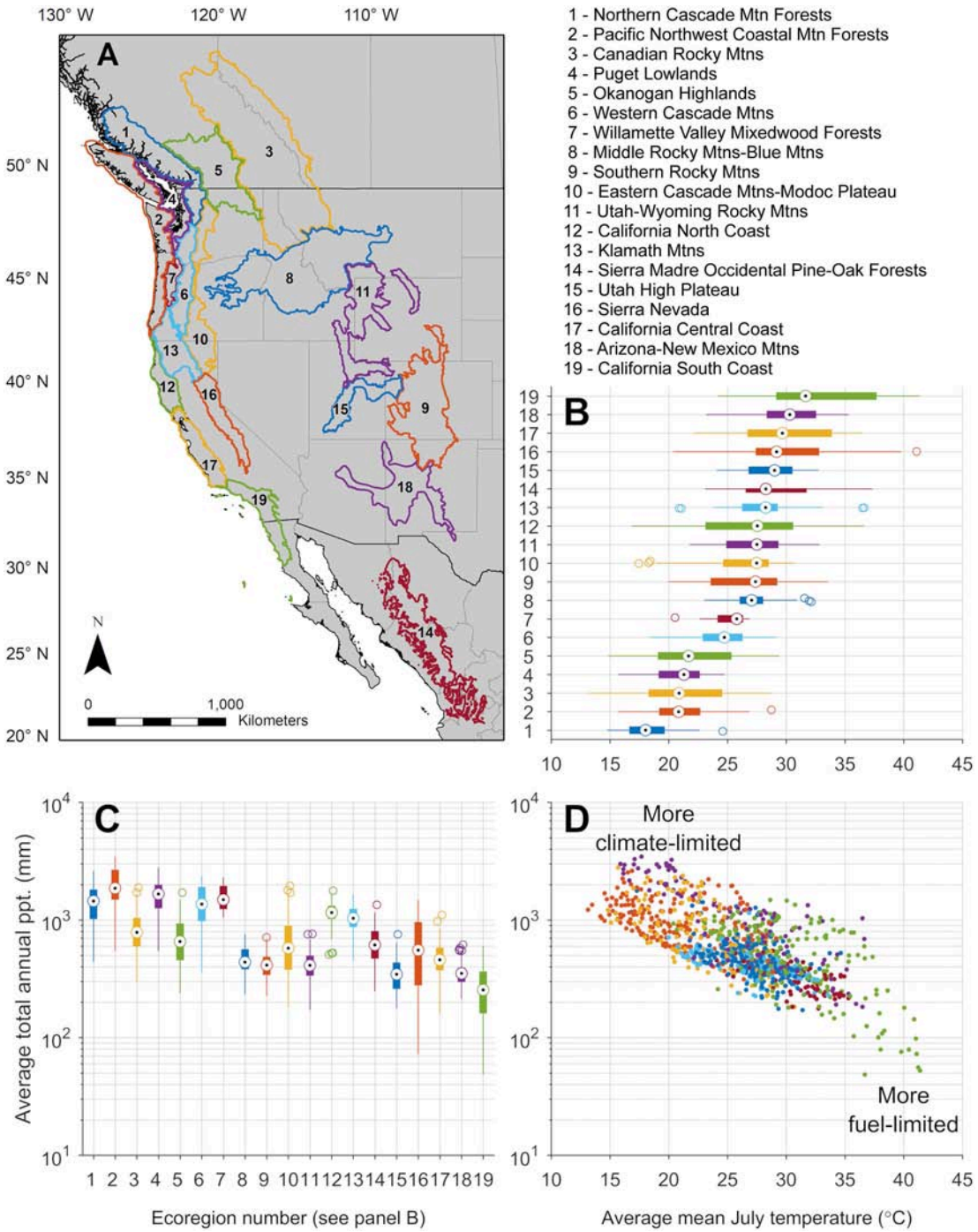

FIGURE 3 | Climatic ecoregions of western North America referenced in the text, in geographic **(A)** and climate space **(B–D)**. Ecoregions are organized in **(B)** by increasing average mean July temperature, from bottom to top; the same ordering is used in **(C)** for average total annual precipitation, from left to right. Globally, these two climate variables are the most relevant for predicting fire presence/absence (Krawchuk et al., 2009). Values in **(B,C)** define climate space **(D)** occupied by each 0.5 degree latitude grid cell, in each ecoregion. Ecoregions are based on Bailey (1998) but subdivided in The Nature Conservancy Terrestrial Ecoregions (Olson and Dinerstein, 2002). Climate data are from the Climate Research Unit (New et al., 1999), represent 1961–1990 average values, with a 0.5° spatial resolution.

climate-limited, burned area will likely increase in the near term. Warmer-drier summers already facilitate greater burned area due to increased frequency and duration of seasonal droughts, which increases fuel availability to burn (Holden et al., 2018). Significant fuel accumulation and lower fuel moisture within a fire season will increase fire severity, which could reduce seed

availability for post-fire regeneration. As landscapes burn more frequently, forests with previously climate-limited fire regimes will see a decrease in woody fuels as they are consumed by fire (*cf.* Littell et al., 2018), and postfire revegetation by forest tree species slows. At the same time, these forests could see increased grass and herbaceous fuels. Forest resilience to high-severity wildfires is thus expected to change where fire is currently climate-limited, with recovery to forest potentially taking longer than observed over the twentieth-century, or not occurring at all (Davis et al., 2018; Stevens-Rumann et al., 2018). In ecosystems where fire is fuel-limited, an increased water deficit will likely decrease productivity and future burned area (Krawchuk and Moritz, 2011; McKenzie and Littell, 2017; Littell et al., 2018). Dry forests at lower elevations and in lower latitudes may see their fire regimes become even more fuel-limited, and some may transition to non-forest with invasive or non-invasive annuals and high-frequency, high-severity fires. For those hybrid ecosystems that characteristically supported moderate-severity fire, and in forests where high tree densities reflect natural postfire cohorts (Schoennagel et al., 2004), increased moisture deficits could lead to increasing fire severity, especially where prior land use and fire suppression have contributed to fuel ladders and elevated surface fuels. These ecosystems are particularly vulnerable to wildfires, as species traits that historically conferred resistance to low- and moderate-severity fires neither provide resistance nor resilience to crownfires.

RESILIENCE AND RESISTANCE IN WESTERN NORTH AMERICAN FORESTS

British Columbian Forests

The westernmost province in Canada, British Columbia (BC), covers 94 million ha, including 60 million forested hectares. The province is physiographically diverse, spanning 10 degrees of

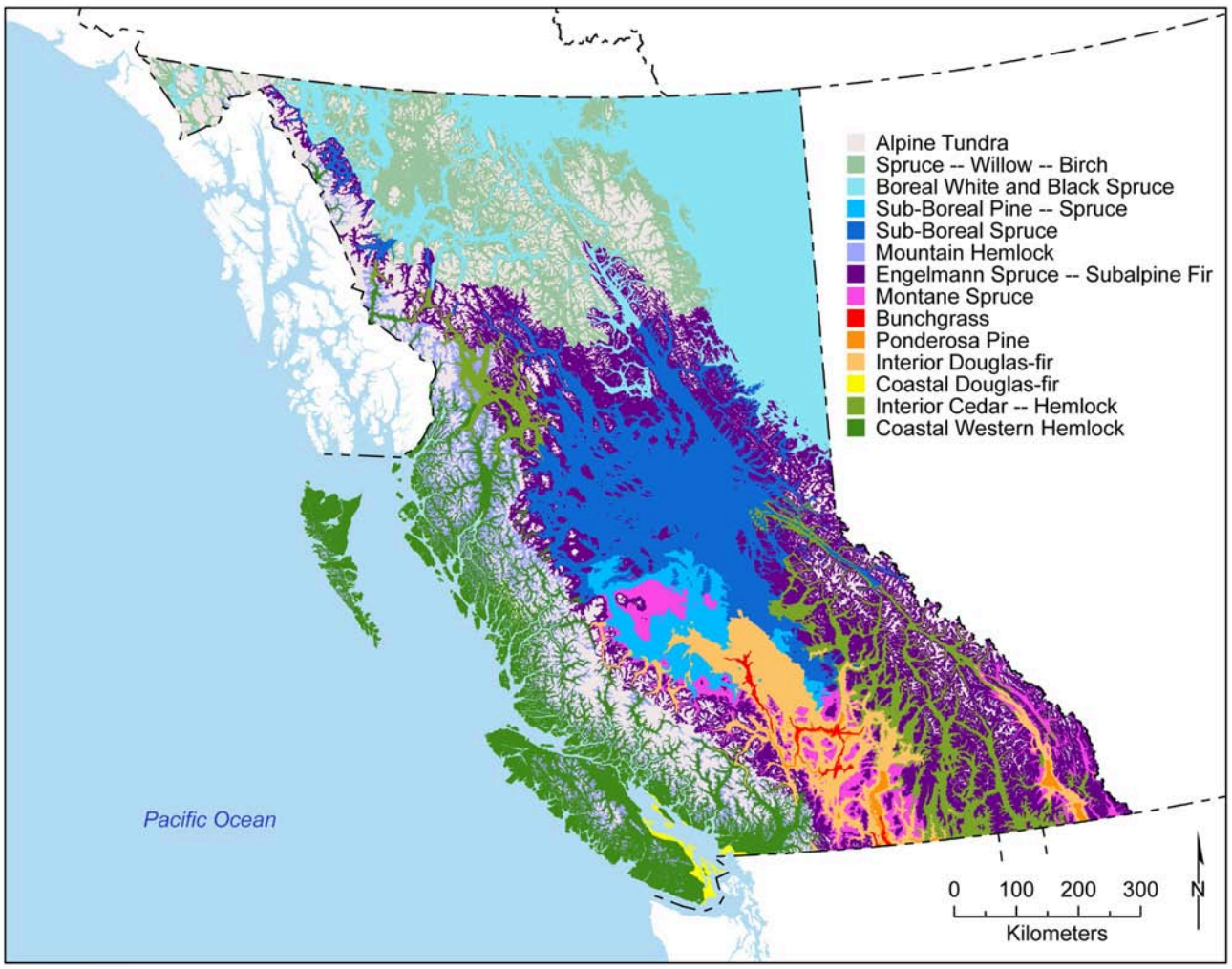

FIGURE 4 | Biogeoclimatic zones of British Columbia (Meidinger and Pojar, 1991). Alpine Tundra includes the Boreal Altai Fescue Alpine, Coastal Mountain-heather Alpine, and Interior Mountain-heather Alpine zones. Data source: British Columbia Ministry of Forest Lands and Natural Resource Operations; map by Raphaël Chavardès and Shuojie Li).

latitude, and the Coast, Cascade, and Rocky Mountain ranges (**Figures 2**, **3**, M333, M211a, M211b, M242, M245, M132a, M132b). It encompasses 16 biogeoclimatic zones (Meidinger and Pojar, 1991, **Figure 4**) with diverse ecosystems including coastal temperate rainforests, grasslands, and cold subalpine forests, which reside along broad latitudinal and elevational gradients of temperature and precipitation.

East of the coastal forests and mountains (**Figure 4**), pre-management era disturbance regimes were complex and variable, with fire as a dominant agent (Boulanger et al., 2014). In plateau and mountain dry mixed-conifer forests (interior Douglas-fir often mixed with lodgepole pine (*P. contorta*) and occasionally ponderosa pine and western larch in extreme southern BC), historical moderate-severity fire regimes included frequent surface fires at the lowest elevations, transitioning to infrequent crownfires at higher elevations (Marcoux et al., 2013, 2015; Chavardès and Daniels, 2016; Greene and Daniels, 2017). Crownfires in subalpine forests commonly yielded even-aged lodgepole pine forests, or lodgepole, subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) mixes. Crownfires in sub-boreal forests likewise yielded even-aged lodgepole pine, or lodgepole dominated mixes similar to subalpine forests, but also with white birch-*Betula papyrifera*, white spruce-*P. glauca*, quaking-*Populus tremuloides*, and bigtooth aspen-*P. grandidentata*. Although trees with multiple fire-scars indicate the presence of moderate-severity fires, for the most part, moist forests exhibited complex structure with old trees, indicating long fire-return intervals (Courtney Mustafi and Pisaric, 2014; Marcoux et al., 2015). In general, high-severity crownfires dominated in sub-boreal and boreal forests (white and/or black spruce-*P. mariana*), but there was also evidence of abundant tree island remnants and spatial complexity after fires linked to subtle topographic and fire behavior variability and proximity to wetlands and lakes (Andison and McCleary, 2014; Krawchuk et al., 2016). Entangled with fire, episodic insect outbreaks were also common across most forest types (Burton and Boulanger, 2018), and owing to complex successional patterns, most outbreak events were small (10^0-10^2 ha) to medium-sized (10^2-10^4 ha), but most acres were affected by the largest events ($>10^4$ ha, Aukema et al., 2006).

In BC, burned area is primarily controlled by annual to decadal climate and fire weather; fuels are typically not limiting. However, fuel availability to burn strongly influences fire severity. Recent fires in 2017 and 2018 exhibited extreme behavior and exceeded suppression capabilities across most forest types; more than 1.2 million ha burned in both years. Several lines of evidence reveal that fire exclusion–which reduced forest seral stage heterogeneity (**Figure 5B**)–and subsequent insect outbreaks have reduced forest resilience and resistance to contemporary fires, with the degree and particular drivers varying among ecosystems. For example, fire scar records from plateau and mountain forests show the near elimination of fires starting in the late 19th- to early 20th-centuries (Marcoux et al., 2015; Greene and Daniels, 2017; Harvey et al., 2017). The colonization by Euro-Canadians during this time ended frequent cultural burning by indigenous people (Christianson, 2015;

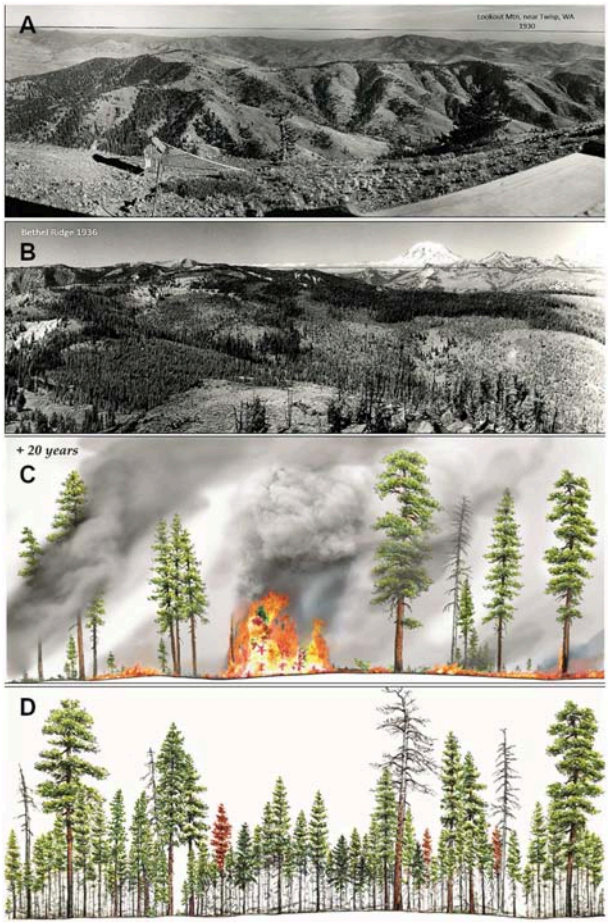

FIGURE 5 | (A) Landscapes were hierarchically nested throughout ecoregions of western North America. Broad-scale physiognomic patchworks formed the upper level. Grasses, herbs, and/or shrubs were the primary fuels, which tended to perpetuate a frequent grass-fire cycle, often yielding mollisols. This broad-scale patchwork functioned as a relatively fast fire delivery system by day, and by night as a fire spread dampening system, where fuel moistures recovered with the night-time relative humidity. Presence of this non-forest-forest patchwork afforded a broad-scale resilience context for the embedded forest. Fires delivered to the forest edge were more often relatively low energy in comparison to modern-era fires. **(B)** Forest successional landscapes occurred at a meso-scale, and they resided within the larger physiognomic landscape. Forest successional conditions varied by time since fire and reburn frequency. Where reburning was common and reburned patches were small to medium sized, forest successional conditions developed with little or no woody surface fuels, which later led to a low probability of crownfire initiation in the event of a wildfire. With increasing time since fire, forests would encroach on larger grass, shrub, and woodland patches. In areas with long time since fire, forest successional conditions would become more homogeneous, with forest density and layering increasing within and among forest successional patches. Variability in surface fuels and forest successional conditions influenced variability of fire severity and sizes of fire severity patches, which increased both the resistance and resilience of the forest successional landscape. **(C)** At a relatively fine scale, patches functioned as small landscapes within the larger successional landscape. Especially in dry and moist mixed conifer patches with low or moderate severity fire regimes, tree regeneration and mortality patterns were clumped and gapped, with both clump and gap sizes roughly following an inverse-J distribution. Frequent to moderately frequent wildfires (e.g., every 5–30 years,

(Continued)

FIGURE 5 | the illustration shows +20 years since the last fire) would thin out patchy surface fuels fallen since the previous fire, and burn out clumped fuel ladders and individual seedlings, saplings, and poles regenerated since the last fire. This clumped and gapped tree distribution and pattern of fire severity and tree mortality was resilient and self-maintaining under most conditions, and provided resistance to severe fires. **(D)** Absent frequent fires and regular fuel consumption, patches filled in with regenerating trees, fuel ladders accumulated, and resistance and resilience both collapsed. Panels **(C,D)** are reprinted with permission of Robert Van Pelt.

Lewis et al., 2018). This, along with fire suppression–preceded by extensive agriculture and livestock grazing–encouraged the expansion of forest cover but reduced flashy fuel continuity and limited fire spread. Absent these fires, changes are evident at patch to broad ecoregional landscape levels. Patch-level changes included accumulation and persistence of dense, understory canopy layers, ingress of seedlings, saplings and poles to form ladder fuels, and accumulation of woody surface fuels (Marcoux et al., 2015; Chavardès and Daniels, 2016). These changes collectively reduced resistance to high severity fires and the likelihood of low- and moderate-severity fires within patches, and increased likelihood of crownfire initiation and spread within and among patches (**Figures 5C,D**). Understanding and reversing the extent of these developments is a key to restoring resistance and more characteristic patch-level fire behavior.

At local and ecoregional landscape levels, the structure and composition of dry and some moist mixed-conifer forests (interior Douglas-fir, often with lodgepole pine and western larch) has shifted toward closed-canopy, late-seral conditions composed of fire-intolerant species (Douglas-fir, grand fir-*A. grandis*, and subalpine fir), while surface and canopy fuels have become more homogeneous and contagious along elevational gradients (Marcoux et al., 2015; Stockdale et al., 2015; Chavardès and Daniels, 2016). Today, forests are increasingly vulnerable to large spreading crownfires and beetle outbreaks. Restoring open canopy conditions with fire tolerant species and limited surface fuels (**Figure 5C**), especially in drier topoedaphic settings, is crucial to restoring more crownfire resistant stand and landscape conditions. In both plateau and mountain forests, discerning the relative importance of surface vs. crownfire effects in historical moderate-severity fire regimes remains a work in progress.

Given long fire return intervals and prevalence of crownfires in the historical fire regimes of subalpine, sub-boreal, and boreal forests, fire suppression impacts are less clear within patches relative to landscapes. However, fire suppression along with climate change and management that emphasized widely distributed mature lodgepole pine forest conditions for timber harvest is implicated in the 1999–2015 mountain pine beetle (*Dendroctonus ponderosae*) outbreak (Carroll et al., 2004; Raffa et al., 2008), which affected 18.3 million ha, and was most severe in sub-boreal forests (Province of British Columbia., 2018). Over the course of the 20th-century, fire suppression eliminated most wildfires, which would have maintained heterogeneity in pre-forest and nonforest lifeform patterns, and forest seral stage, age class, and density conditions (**Figures 5A,B**), all of which contributed to forest resilience. Absent fires, lodgepole pine trees aged, patches blended with their neighbors, and large forest extents became vulnerable to mountain pine beetle outbreaks (Raffa et al., 2008). Over the last two decades, more than half of BC's merchantable pine volume was killed by bark beetles (731 million m^3, Province of British Columbia., 2018), leading to extensive tree salvage operations. Restoring characteristic heterogeneity in lifeform and forest seral stage patchworks is a key to future wildfire and climate change adaptation and resilience of sub-boreal forests.

Fuel hazards perpetuated by modern forest management, including harvests without prescribed burning of silvicultural activity fuels, have reduced forest resistance and resilience to wildfires by amplifying surface fuels and not treating fuel ladders, but hazards could be mitigated (Stephens et al., 2016). BC forest management could benefit from incorporating knowledge of natural fire regimes and cultural burning. Likewise, the BC fire regime classification–developed in the 1980s and 1990s and based on expert knowledge—overstates the role of stand-replacing disturbances in initiating succession, in all but valley bottom and alpine ecosystems (Andison and Marshall, 1999; Daniels and Gray, 2006; Marcoux et al., 2013). This model is used to justify broad application of fire suppression and clearcut silviculture to protect timber supplies, which has led to simplified age-class and patch size distributions, and decreased landscape resilience.

Forest management that is focused on stand-level timber production goals is disconnected from the current reality of increasing landscape vulnerability to wildfires in a changing climate. For example, it is routine practice to remove abundant patches of aspen and birch via silvicide application or pre-commercial thinning to favor lodgepole pine. These hardwood patches were influential to blocking wildfire flow on the landscape under many fire weather conditions. Their restoration and amplification would be an important wildfire adaptation going forward. The current practice of planting dense lodgepole pine monocultures enhances vulnerability to large-scale future bark beetle outbreaks. Plans to increase planting densities to sequester more carbon will likely result in elevated bark beetle and wildfire-related carbon losses, rather than gains (Hurteau and North, 2009). A diversified provincial wildfire management strategy was introduced in 2012 to protect human life and resource values at risk, and to encourage sustainable, healthy and resilient ecosystems (BC Wildfire Management Branch Strategic Plan., 2012). However, lacking a strong conceptual framework, implementation has been slow, leaving communities vulnerable to both wildfire and climate change.

Inland Pacific Northwest Forests

The Inland Pacific Northwest (PNW) region displays widely varying biophysical conditions and vegetation types, with areas of Mediterranean and continental climate superimposed on strong west-east temperature and precipitation gradients. Residing in a rain shadow created by the crest of the Cascade and Klamath Mountains, the region hosts several distinct provinces (**Figures 2, 6**): the Okanogan Highlands (M333), the southern and eastern portions of Northern and Southern Cascade Mountains (M242), the Blue Mountains (M332), and the Upper Klamath Mountains

(M261). Within the interior portions of these provinces, elevation gradients range from semidesert (150 m) to alpine (4,392 m), and dominant lifeform, productivity, growth, and successional patterns are driven by plant-available water (principally from snowpack), temperature, solar radiation, and disturbance.

This interplay of temperature and precipitation gradients, elevation and aspect, created landscapes of intermingled forest type and wildfire regime (**Figures 6C,D**). Dry forest (pure ponderosa pine and pine mixed with Douglas-fir and/or grand fir) and woodland (≤20% tree cover, ponderosa pine, Garry oak-*Quercus garryana*, and western juniper-*Juniperus occidentalis*) patches typically experienced low- and some moderate-severity burns at 5–25 year intervals (Hessl et al., 2004). Moist forests (western larch, ponderosa pine, Douglas-fir, and grand fir) also experienced low- and moderate-severity burns, but with a greater proportion (20–25%) at high-severity, owing to often longer (25–50 year) intervals (Hessburg et al., 2007). Cold subalpine forests (Engelmann spruce, lodgepole pine, and subalpine fir mixes) typically experienced moderate- and high-severity burns at 75–150 year return intervals; however, reburning occasionally reinforced low- or moderate-severity fire (Prichard et al., 2017). Combined with extensive aboriginal fires (Boyd, 1999; White, 2015), the result was an intermingling of forest and non-forest cover types, and assorted seral stages (**Figures 5A,B**).

In addition to driving composition and successional conditions of forests, wildfires created and maintained an ever shifting broad-scale patchwork of grass-, shrub-, and woodland (including pine, oak, and juniper) conditions. Aerial photographs from the early 20th-century show that the combined non-forested area averaged 46% (range 25–71%) of the region (Hessburg et al., 2000, 2016, **Table 1**; **Figures 5A,B**, **7**). Frequent fires likely reduced total forest area and perpetuated woodlands and grasslands, which consequently supported high fire spread rates and low flame length and fireline intensity (Hessburg et al., 2016). This resilient mosaic that included non-forest types likely delivered fire into dry and some moist forests maintaining tree densities well below carrying capacity (Hagmann et al., 2014). Thus, lifeform patchworks were important for creating and maintaining resilience to disturbance across broad landscapes.

A defining characteristic of the region's forests that conferred resilience was its hierarchical structure. Fire and local climatic conditions maintained dynamically shifting broad-scale patterns of forest and non-forest. Within dry and many moist forest patches, fire, insect, pathogen, and weather disturbances created and maintained fire-resistant, multi-aged and unevenly spaced arrangements of individual trees, and small- to moderate-sized tree clumps interspersed with openings of various sizes (**Figure 5C**, Larson and Churchill, 2012; Churchill et al., 2013). Many low- and moderate-severity fires, and some high-severity fires, left a backbone of medium (40–64 cm) to large (>64 cm) diameter, older, fire- and drought-resistant trees (Hessburg et al., 2015), which provided a high degree of genetic diversity and seed sources for regenerating future forests (Hamrick, 2004). These nested conditions provided patch scale resistance to severe wildfires because cross-scale discontinuity of fuels and host trees reduced the likelihood of large crownfires and insect outbreaks. Interspersion and cross-scale linkage among non-forest and forest seral stage conditions, along with tree clumps and openings within forest patches, also provided an exceptional range of habitats in close proximity. Such hierarchical patterning increased plant species diversity of adjacent understory communities, promoted regeneration of fire-tolerant tree species, and increased the duration of snow cover (Lundquist et al., 2013).

Past forest management and fire exclusion have reduced forest resistance and resilience to disturbances and climatic warming. Contributing factors include the forced displacement of aboriginal peoples and termination of their intentional burning; livestock grazing that reduced grass cover and fine fuels, and improved tree establishment; selective logging of large, thick-barked, fire-tolerant ponderosa pine, western larch, and Douglas-fir; and aggressive fire suppression (Hessburg and Agee, 2003; Hessburg et al., 2005). Absent fire, thin-barked and shade-tolerant small-diameter (10–40 cm) Douglas-fir and grand fir broadly recruited in understories, forming dense, multi-layered conditions in most managed dry and moist mixed-conifer forests (**Figure 5D**). These changes favored expansion of native defoliator (western spruce budworm, Douglas-fir tussock moth), and bark beetle outbreaks (Douglas-fir beetle-*D. pseudotsugae*, western bark beetle-*D. brevicomis*, and fir engraver beetle-*Scolytus ventralis*), and contribute to large influxes of woody surface fuel. On dry plateau and foothill sites, these changes fostered forest encroachment into former grass-, shrub-, and woodlands, and development of often dense multi-layered pine, oak, and juniper forests (Hagmann et al., 2014, 2019). Historical conditions characterized by variable patterns of physiognomic types, forest seral stages, and tree clumps and openings are now homogenized in many places, and the backbone of large, old, fire-tolerant trees has been diminished by logging, bark beetles, and high-severity fires. Collectively, these changes have increased potential for large crownfires and drought-related insect outbreaks (Hessburg et al., 2005), trends that are already witnessed across the region. Reversing these trends and restoring the hierarchical life-form patchworks that once defined this region's forests will be key to restoring multi-scale resilience and resistance. Documenting the natural range of variation in these conditions would inform restorative actions (Landres et al., 1999; Keane et al., 2009).

Today's forests are vulnerable to ongoing climate change (Littell et al., 2009; Cansler and McKenzie, 2014; Reilly et al., 2017). Through expansion of forest area and closed-canopy conditions, patch-level resistance, once instrumental in maintaining low- or moderate-severity fire and localized insect outbreaks, has been eliminated in many places. Large stand-replacing fires have, in some places, shifted broad-scale dominance from conifers to fire-adapted shrubs or hardwoods, while in other places, have synchronized regeneration of fire-adapted trees with serotinous cones. In both cases, the effect has been to simplify species composition and perpetuate a high severity fire regime.

The region is at a crossroads; restoring forest resilience to wildfire and climatic warming will require increasing the footprint of treatments and allowing managed wildfires to burn

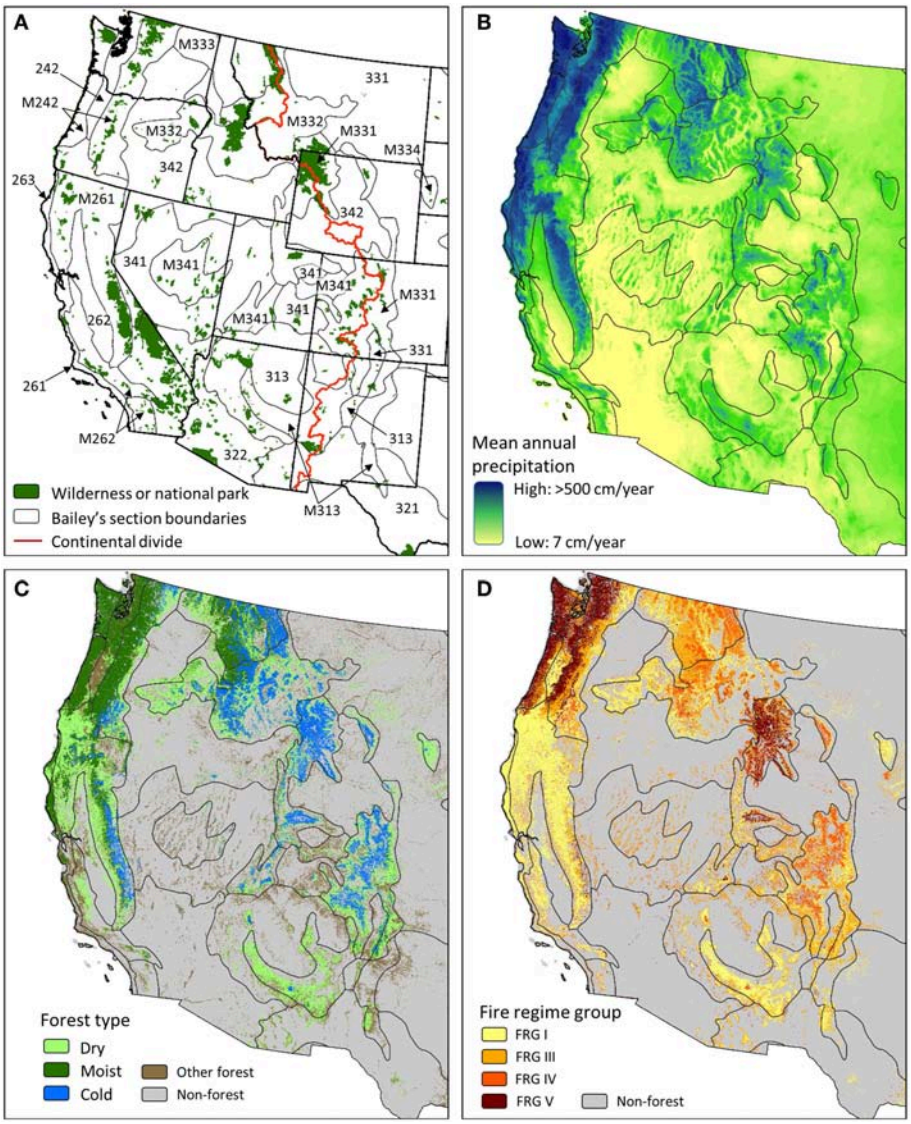

FIGURE 6 | Maps depict **(A)** protected areas (designated wilderness and national park) and section-level ecoregion boundaries, **(B)** mean annual precipitation, **(C)** forest types, and **(D)** fire regime groups (FRGs) for the contiguous western US. The "other forest" type in panel **(C)** includes forest types that are not addressed in this paper, such as pinyon-juniper woodlands and riparian forests. FRG classes are FRG I: fire return interval ≤ 35 years, low and mixed severity; FRG III: fire return interval 35–200 years, low and mixed severity; FRG IV: fire return interval 35–200 years, replacement or high-severity; FRG V: fire return interval > 200 years, any severity. Portions of the study area that extend into Mexico and Canada are not shown because not all datasets are coextensive to these regions. Data sources: Bailey sections—(Bailey, 1998); **(B)**—(Daly et al., 2008); **(C,D)**—(Rollins, 2009) (www.landfire.gov).

under certain circumstances to restore fire and the myriad ecosystem functions it supports. Efforts are underway to restore more resilient patterns of forest structure, composition, and fuels, and they are increasing adaptive capacity of many landscapes by reducing forest vulnerability to drought and uncharacteristic high-severity fire events (WA DNR., 2017). However, current efforts are limited by policies that are risk-averse to managed wildfires, mistrust among some partners and stakeholders, insufficient social license to implement treatments, and institutional norms that discourage broad use of prescribed and managed wildfire and mechanical thinning (Spies et al., 2018a). Meanwhile, ongoing aggressive fire suppression facilitates uncontrollable wildfires during periods of extreme fire weather, which drives a majority of fire effects. Adapting the region to a warmer climate will require leadership that enables deep dialogue among community partners about key landscape changes, changes to disturbance regimes, and growing effects of climate change. This information can be used within structured decision-making processes (*sensu* Gregory et al., 2012), whereby trade-offs in ecosystem structure and function can be considered alongside human community values and needs, resulting in broad landscape-level restoration prescriptions that leave both communities whole.

TABLE 1 | Area of nonforest, pre-forest (=early seral), and mid- to late-seral conditions in 5 Inland Northwest provinces (**Figure 7**) shown by potential vegetation group.

Province	Potential vegetation group (% Area)								
	PP	DMC	MMC	DCF	MCF	Other forest PVGs	Herb/shrub	Non-Vegt	% of province
NORTHERN GLACIATED MOUNTAINS									
Non-forest = herbland + shrubland + woodland + bareground + stand initiation forest	88.9	40.2	36.5	28.6	35.5	43.1	98.7	99.8	**43.5**
Mid + late-seral forest	11.1	59.8	63.5	71.4	64.5	56.9	1.3	0.2	**56.5**
% PVG area	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
% province area	0.3	7.9	16.1	7.3	39.8	18.5	7.9	2.2	100.0
NORTHERN CASCADE MOUNTAINS									
Non-forest = herbland + shrubland + woodland + bareground + stand initiation forest	82.1	27.9	19.8	43.9	36.0	27.5	99.9	99.4	**41.8**
Mid + late-seral forest	17.9	72.1	80.2	56.1	64.0	72.5	0.1	0.6	**58.2**
%PVG area	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
% Province area	1.8	10.4	24.3	3.0	14.9	27.0	12.8	5.8	100.0
BLUE MOUNTAINS									
Non-forest = herbland + shrubland +woodland + bareground + stand initiation forest	82.0	38.8	22.8	43.6	26.5	84.7	99.1	91.8	**48.5**
Mid + late-seral forest	18.1	61.2	77.2	56.4	73.5	15.3	0.9	8.2	**51.5**
% PVG area	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
% Province area	3.9	9.7	46.3	4.1	8.1	3.6	24.1	0.1	100.0
UPPER KLAMATH MOUNTAINS									
Non-forest = herbland + shrubland + woodland + bareground + stand initiation forest	75.1	89.5	19.9			48.6	99.9	100.0	**71.4**
Mid + late-seral forest	24.9	10.5	80.1			51.4	0.1	0.0	**28.6**
% PVG area	100.0	100.0	100.0			100.0	100.0	100.0	100.0
% Province area	24.4	0.8	6.7	0.0	0.0	33.1	33.9	1.1	100.0
SOUTHERN CASCADE MOUNTAINS									
Non-forest = herbland + shrubland + woodland + bareground +stand initiation forest	25.6	23.4	13.3	44.1	27.8	17.3	94.8	99.3	**25.1**
Mid + late-seral forest	74.4	76.6	86.7	55.9	72.2	82.7	5.2	0.7	**74.9**
% PVG area	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
% Province area	35.1	2.1	11.9	0.1	1.4	43.1	2.3	4.0	100.0

Potential vegetation groups on forest capable sites are PP, ponderosa pine; DMC, dry mixed conifer (ponderosa pine Douglas-fir and/or grand fir on dry sites); MMC, moist mixed conifer (ponderosa pine and/or western larch with Douglas-fir and/or grand fir on moist sites); DCF, dry cold forest (lodgepole pine and/or subalpine fir and/or Engelmann spruce on dry, cold, and harsh sites); MCF, moist cold forest (lodgepole pine and/or subalpine fir and/or Engelmann spruce on moist and cold sites); Other, all other forest PVGs; Herb/Shrub, herbland and shrubland on non-forest sites; and Non-Vegt, bare ground, rock, water, ice. Values in bold typeface summarize the relative percentage of provincial landscapes in non-forest and forest conditions.

Northern Rocky Mountain Forests

The Northern Rocky Mountain (NR) region is distinctive for its broad, high mountain ranges that roughly follow the Continental Divide (**Figure 2**, M331, M332, M333, M334; and **Figure 6A**). It is known for its extensive wilderness areas that encourage management of naturally ignited wildfires. Forests of the region can be described in three broad types (**Figure 6C**): (1) dry pine and dry mixed-conifer (ponderosa pine, often with western larch, Douglas-fir, grand fir, and lodgepole pine), (2) moist mixed-conifer (western larch, Douglas-fir, grand fir, lodgepole pine, with western hemlock-*Tsuga heterophylla* and western redcedar-*Thuja plicata*), and (3) cold forests (subalpine fir, lodgepole pine, Engelmann spruce, occasionally with limber pine-*P. flexilis*, whitebark pine-*P. albicaulis*, and subalpine larch-*L. lyalli*). Within each of these types, there is substantial compositional and structural diversity associated with local climatic gradients, and topographically mediated differences in fire frequency and severity. The climate of the NR is continental; warm-dry summers following warm springs often lead to regionally extensive wildfires (Heyerdahl et al., 2008a; Morgan et al., 2008).

Similar to other interior regions, historical fire regimes varied with forest type (**Figure 6D**). Dry ponderosa pine and mixed-conifer forests experienced frequent (every 5–25 year) low- and moderate-severity fires (Keane et al., 2002); occurrence of stand-replacing fire was relatively uncommon. Moist mixed-conifer forests experienced more infrequent (every 25–50 year) mixed- and high-severity fires (Arno and Davis, 1981). In cold forests, fires were very infrequent (every 100–300 year, Keane et al., 2002), and often high severity. Across all forest types, stabilizing feedbacks between fire and forest vegetation produced either

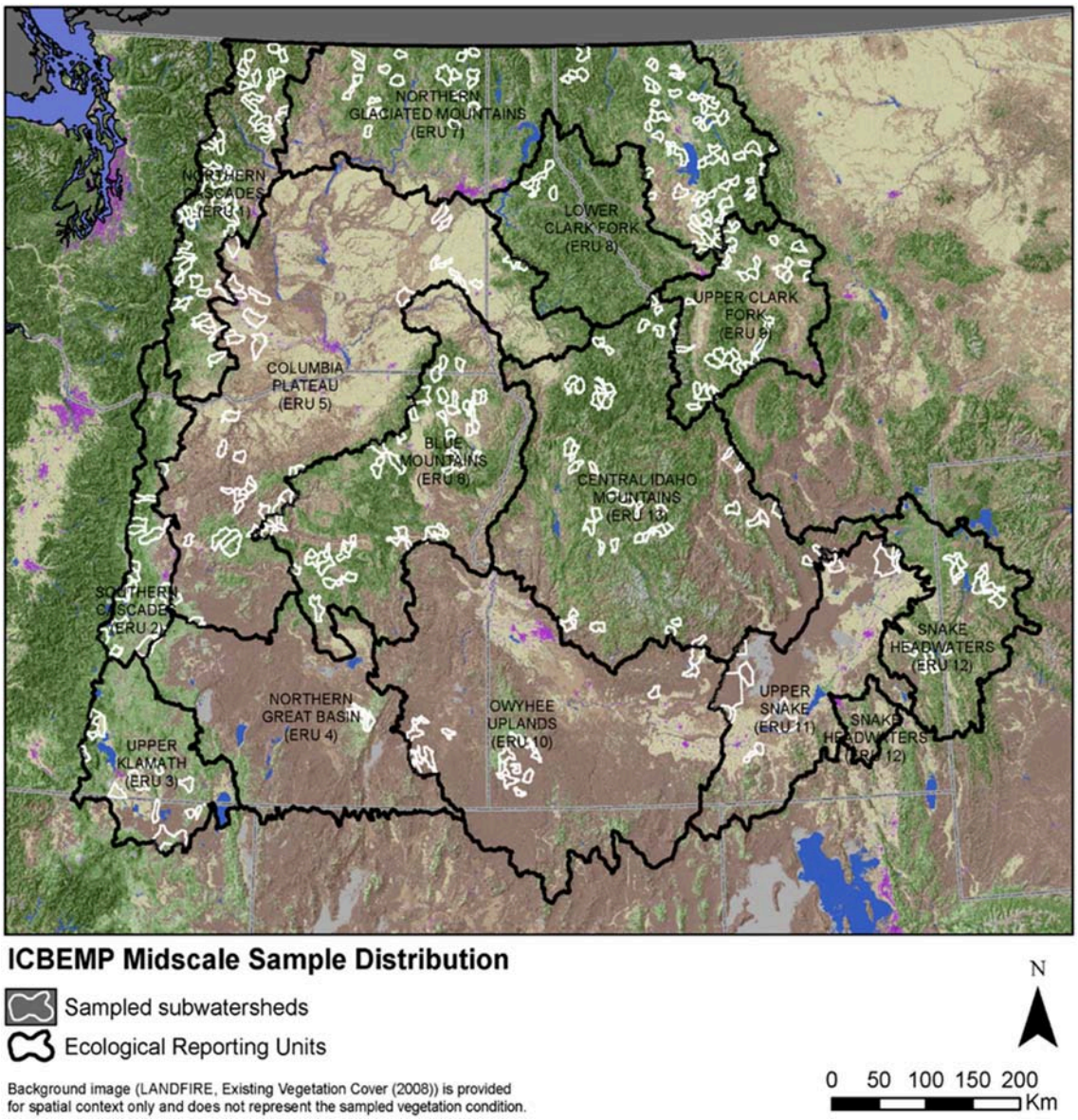

FIGURE 7 | Map of sampled subwatersheds in provinces (Ecological Reporting Units-ERUs) of the Interior Columbia River Basin assessment. Subwatersheds were sampled in a two-stage, stratified random sample of subwatershed conditions of broad province-scale ecological reporting units (ERU's, Hessburg et al., 2000).

a resistant or resilient ecosystem response (Parks et al., 2015), though these feedbacks manifested differently, depending upon whether the fire regime was fuel- or climate-limited, tree species life history traits (Belote et al., 2015), and spatial scale (i.e., patch or landscape). We provide examples of these feedbacks in following paragraphs.

In the dry pine and dry mixed-conifer patches, frequent fire favored fire-tolerant ponderosa pine and western larch, and inhibited in-growth of shade-tolerant and fire-intolerant Douglas-fir. This promoted wildfire resistance within patches through a relatively low density of medium and large diameter trees that were arranged in spatially heterogeneous mosaics of individuals, tree clumps, and openings (Clyatt et al., 2016). The fire regime was primarily ignition driven with frequent fires perpetually limiting fuel accumulation and maintaining a surface-fire dominated regime (Larson et al., 2013) in which fire spread and occurrence were typically self-regulating (**Figure 5C**, Parks et al., 2015).

Owing to lower fire frequency, moist mixed-conifer forests were composed of fire-tolerant ponderosa pine and western larch intermixed with fire-intolerant species like western hemlock and western redcedar; composition varied a great deal within and among stands. Fires burning under mild to moderate fire weather conditions produced moderate-severity effects,

reflecting heterogeneous species assemblages and local variability of fuels and topography. Under dry and windy conditions, fires often overrode species traits, resulting in large high-severity burn patches (Belote et al., 2015). Resilience of large forest landscapes to fire was maintained by cross-scale connections between variable fire effects within patches and highly heterogeneous landscape patterns.

In cold forests, tree species exhibit few traits that confer resistance to fires. There, the fire regime was primarily climate-limited; extensive area burned during years with warm-dry summers and low fuel moisture (Morgan et al., 2008; Higuera et al., 2015), and fires could spread rapidly during high wind events. Fire spread and occurrence were more or less self-regulating, conferring a certain amount of resilience to forests at the landscape level; patterns of prior burned and recovering areas decreased the likelihood of fire ignition and spread of subsequent fires for 1–2 decades (Parks et al., 2015, 2016).

Since the 1880s, forests in the NR have been affected by fire exclusion, timber harvest, and interactions with native and non-native insects and pathogens. As a result of fire suppression and forest management, a once resistant forest composition has shifted away from early seral, shade-intolerant tree species toward late seral, shade-tolerant species (Hessburg et al., 2000; Keane et al., 2002). Dry forest patches have missed several fire cycles, resulting in excessive accumulations of live and dead fuels, and infilling by small diameter, fire-intolerant tree species (**Figure 5D**). Consequently, contemporary fires are often uncharacteristically large and severe, reflecting decreased forest resistance and resilience. Reversing these trends in dry forests is a key to re-establishing more resistant conditions. In moist mixed-conifer and cold forests, fire exclusion reduced abundance of early- and mid-seral patches, affecting landscape fuel and successional patterns, and species composition. These forests are now more prone to large crownfires than was formerly the case. Re-establishing heterogeneity in forest seral stage conditions is critical to restoring wildfire resilience. Determining the natural range of variation in these conditions will be important to informing restorative actions (Landres et al., 1999; Swetnam et al., 1999; Keane et al., 2009).

Past timber harvest likewise altered dry and moist forest structure, composition, and pattern. Beginning in the 1880s, timber harvests removed large-diameter fire-resistant trees, compounding the effects of fire suppression on forest structure and composition (Hessburg et al., 2000; Naficy et al., 2010). Regeneration harvests of the 1950s and 1960s also affected cold forests, where dispersed clearcutting and associated road building fragmented the landscape, shifted patch-size distributions, and disrupted feedbacks between fire spread and fire history. White pine blister rust profoundly changed moist and cold forests too. Caused by an introduced pathogen, widespread infection resulted in the collapse of western white, whitebark and limber pine populations throughout western North America, altering the composition of moist and cold forests (Maloy, 1997). In cold forests, both lodgepole and whitebark pine have been impacted by climate-driven eruptions of the mountain pine beetle that may be outside the range of historical variability (Logan et al., 2010).

Climate change is an additional stressor of dry, moist, and cold forests. Increasing summer temperatures and decreasing summer precipitation will likely increase area burned (Higuera et al., 2015; McKenzie and Littell, 2017; Holden et al., 2018; Littell et al., 2018). While postfire tree regeneration in recent decades appears sufficient to support forest resilience (Kemp et al., 2016), interactions between fire and drought are increasingly leading to reduced tree regeneration on the driest sites (Stevens-Rumann et al., 2018; Davis et al., 2019), slowing forest succession and causing transitions to non-forest. These changes have the potential to disrupt feedbacks that had maintained forests and their fire regimes for centuries. Dry forests may see reduced tree densities and shifts in species composition, and lower treeline environments may shift upward in elevation (Kemp et al., 2016; Stevens-Rumann et al., 2018). Over longer timeframes, cold and moist forests will likely see more frequent (**Figure 6D**) but less severe fires (Parks et al., 2018).

Maintaining and enhancing resilience is feasible in the NR. Certainly, shifts in forest types and fire regimes are expected with a warming climate, but fire, especially managed wildfire, will remain key to forest resilience in the region. The relatively sparse human population provides ample opportunities for managed wildfires. In backcountry areas, a history of managed wildfires has maintained stabilizing feedbacks that promote resilience at stand and landscape levels (Larson et al., 2013; Parks et al., 2015). In areas where these feedbacks have been disrupted, managed wildfire may be integrated with restorative treatments to reinforce these more stabilizing influences (Hessburg et al., 2015).

Southern Rocky Mountain Forests

The Southern Rocky Mountains region (SRM; M331, **Figures 2**, **6**) extends from southern Wyoming through Colorado, and into northern New Mexico. Forests span elevations from 1,600 to 4,000 m and include steep, dissected mountains, high plateaus, and intermountain basins. Varied topography, prevailing westerly winds, and monsoonal precipitation create wide variability in climate, vegetation, and fire regimes.

Resistance and resilience of SRM forests to wildfires varied widely according to the historical fire regime. In lower montane ponderosa pine woodlands, fires were frequent, and most were surface fires; their intensity and extent were fuel-limited (Sherriff et al., 2014; Brown et al., 2015). Frequent fires were lethal to seedlings and saplings, but not mature trees, resulting in a relatively resistant, open park-like structure, with relatively slow tree attrition and recruitment (**Figure 5C**).

In dry mixed-conifer forests (ponderosa pine and Douglas fir, with lodgepole pine and aspen), the fire regime was more complex, including low-, moderate-, and high-severity patches, which resulted in highly variable patchworks of tree species, sizes, and densities, along with non-forest openings (Sherriff et al., 2014; Battaglia et al., 2018). Dry mixed-conifer forests were characterized by high structural diversity, and included a mix of species that resulted in a gradient of resistance and resilience to fire. For example, thick-barked ponderosa pine and Douglas-fir enhanced the resistance of these forests to low-severity fires, while the regeneration strategies of aspen and

lodgepole pine made these forests resilient to high-severity fires. Infrequent occurrence of large and severe fires, often associated with extreme drought, contributed to landscape heterogeneity by creating large, long-lasting non-forest openings (Brown et al., 1999; Huckaby et al., 2001). As in other ecoregions, diversity of lifeform patterns, nested forest successional patterns and varied species composition likely influenced high spatial diversity in the mix of fire and forest insect outbreak severity.

Moist mixed-conifer forests of the upper montane zone consist of Douglas-fir, white fir, lodgepole pine, aspen, Engelmann spruce, and subalpine fir. These forests were also characterized by a variable severity fire regime, including low-, moderate-, and high-severity patches, which resulted in heterogeneous patterns of species assemblages and seral stage conditions (Tepley and Veblen, 2015). Lodgepole pine and mixed Engelmann spruce and subalpine fir forests experienced infrequent (100–300^{+} years) high-severity fires (Higuera et al., 2014; Calder et al., 2015), typically under conditions of extreme drought (Schoennagel et al., 2005). While lodgepole pine typically recovered quickly after fire (Dunnette et al., 2014), spruce-fir forests recovered more slowly–often taking decades to more than a century.

Modern-day SRM forests reflect complex patterns of human impact, including widespread intentional burning during severe 19th-century droughts, followed by 20th-century fire exclusion, domestic livestock grazing, and logging (Kitzberger et al., 2007; Sherriff et al., 2014; Battaglia et al., 2018). In the lower montane pine zone, fire exclusion has resulted in increased forest density and higher fire severity. In upper montane moist mixed-conifer forests, widespread high-severity fires and 20th-century logging have created forests with small diameter trees and elevated fuel continuity (Sherriff et al., 2014; Battaglia et al., 2018). In high elevation lodgepole pine forests, widespread burning and logging in the late 19th century created bark beetle susceptible forests, which have experienced episodic large outbreaks during recent droughts (Chapman et al., 2012; Hart et al., 2015).

Warming temperatures, drought, and below average snowpack since the late-1990s have resulted in increased wildfire and bark beetle activity across all forest types. Moreover, there has been a steady decline in the resilience of ponderosa pine and dry mixed-conifer forests attributable to removal of seed sources by large high-severity fires, and moisture-limited regeneration at low-elevation sites (Stevens-Rumann et al., 2018). A warmer, drier climate in the 21st-century exposes these forests to an increasing number of large, high-severity fires. Limited seed sources and drought will likely slow or limit recovery, resulting in some conversions from forest to non-forest conditions after fires (Andrus et al., 2018). Lower elevation forests are also increasingly susceptible to invasion by invasive annual grasses which contribute to even greater fine fuel continuity and more frequent grass-driven fires.

In contrast, there is resilience to insect outbreaks in some dry and moist mixed-conifer forests due to the presence of advanced hardwood or conifer regeneration (Pelz et al., 2015). Thus, while wildfires and bark beetle outbreaks will continue to increase in frequency and severity with a warming climate, negative feedbacks of short-term aspen dominance and greater abundance of young beetle-resistant trees will likely buffer the extent and frequency of some future fire and beetle disturbances (Hart et al., 2015).

Recent and ongoing declines in forest resilience under climate warming have major societal implications (Calkin et al., 2014). Water is a precious commodity in the arid West, and many of the rivers that supply water to the SRM originate in these forests. Severe wildfires increase soil erosion and sedimentation of water supply systems, necessitating expensive remediation. Exurban development into forests continues at a brisk pace, resulting in continued pressure to suppress all fires.

Current forest management in the SRM is informed by a robust understanding of forest resilience and resistance mechanisms, and of the historical ecology. This knowledge is being implemented to address problems posed by rapid exurban development into fire-prone ecosystems. Prescribed burning programs to reduce surface fuels and maintain dry forest treatments are widely accepted (Fernandes and Botelho, 2003), but often limited in extent due to wildland-urban interface and smoke concerns, as well as costs of removing non-merchantable trees (Addington et al., 2018). In backcountry areas, managed wildfire is an increasingly used and accepted practice to increase landscape heterogeneity, improve resilience, and buffer against subsequent fires and bark beetle outbreaks. Efforts are underway to increase landscape resilience by increasing landscape heterogeneity with variable-density thinning, creating openings in forests, and by favoring drought- and fire-adapted tree species, but many challenges remain.

Klamath and Southern Cascade Mountain Forests

The Klamath and Southern Cascade Mountain regions (**Figures 2**, **6**, M261) are influenced by a Mediterranean climate, with strong west-east precipitation and temperature gradients. The modern climate was established ca. 3,000–4,000 year ago, and climate has been the dominant driver of fire activity throughout the Holocene (Briles et al., 2008; Skinner et al., 2018). Elevation gradients in the deeply dissected Klamath Mountains are strong, controlling local and regional climate patterns. Prominent ridge systems occur between 1500 and 2200 m, and elevations range from 30- to 2755-m (Skinner et al., 2018). With volcanic peaks rising from basalt plateaus, the Southern Cascade Range is geologically younger than the Klamath Mountains, and elevations range from 60-m in the foothills to 4,317-m on Mt. Shasta (Skinner and Taylor, 2018). In both regions, forests are dominated by conifers but often include a mixture of evergreen and deciduous hardwoods. Fire-dependent shrubs are common in both regions, but evergreen hardwoods are more prevalent in the Klamath Mountains.

The Klamath Mountains harbor some of the most diverse forests in the western US (Michael et al., 1993). There, high spatio-temporal variability in fire regimes at local and landscape

levels contributes to a regional biodiversity hotspot. Prior to Euro-American settlement, topography strongly influenced fire regime characteristics, with elevation establishing gradients in fire frequency from high to low, across dry, mesic, and cold forest types, respectively. In dry ponderosa pine and dry and moist mixed conifer forests (**Figure 6C**), fires were compartmentalized by ridgetops, north to south aspect changes, riparian zones, and surface lithology. Dry mixed conifer forests included ponderosa pine mixed with Douglas-fir, white fir-*A. concolor,* incense cedar-*Calocedrus decurrens*, western juniper-*Juniperus occidentalis*, and blue-*Quercus douglasii*, Garry-*Q. garryana*, or California black oak-*Q. kelloggii*, or gray pine-*P. sabiniana*. Moist mixed conifer forests included ponderosa or Jeffrey pine mixed with Douglas-fir, white fir, Pacific madrone-*Arbutus menziesii*, chinquapin-*Chrysolepsis spp.*, canyon live oak-*Quercus chrysolepis,* bigleaf maple-*Acer macrophyllum*, black oak, Pacific dogwood-*Cornus nuttallii*, and/or sugar pine-*P. lambertiana*. These compartments burned with similar frequency, yet often in different years. However, in drought years, fires burned across neighboring compartments and landscapes, often unabated, highlighting the varied contributions of bottom-up and top-down controls on fire regimes (Taylor and Skinner, 2003; Taylor et al., 2008). Steep and often narrow ridgetops created contrasting conditions leading to variation in fire behavior and effects. Additionally, the upper third of slopes and ridgetops experienced higher proportions of high-severity fire, and valley bottoms and lower slopes, the lowest (**Figure 8**). The distribution and persistence of fire-dependent shrublands and serotinous cone tree species—some which are narrowly endemic—are linked to landscape level fire severity patterns. Fuel discontinuities in high-elevation glacially-carved landscapes contributed to localized fire refugia, occupied by fire sensitive species and some of the richest conifer assemblages worldwide (Skinner et al., 2018). However, in the gentler topography of the Southern Cascades, common low- and moderate-severity fires were seldom constrained by terrain. Severity patterns instead were influenced by variation in fuel and weather (Skinner and Taylor, 2018).

Fire regimes changed after Euro-American settlement and the advent of fire suppression. In dry and mesic forests, frequent relatively small fires became less frequent and larger, with less change in low frequency fire regimes of cold forests. With suppression and fire exclusion, the reduced fire frequency and extent caused cross-scale changes in patterns of vegetation and fuels, which were most obvious in dry and mesic forests (**Figure 9**). An exception to this general pattern occurs in areas of ultramafic bedrock with species that tolerate nutrient poor soils, where vegetation and fire regimes have remained stable for millennia despite climatic changes (Briles et al., 2008; Skinner et al., 2018). Before fire suppression, fires of variable severity, but tending toward low- and moderate-severity, created high spatial complexity in forest openings, and generally more open-canopy conditions than are typical today. This self-reinforcing heterogeneous pattern enhanced forest resilience but has been replaced by more uniformly dense and layered forests, with more conifers, fewer hardwoods, smaller and fewer openings, and higher fuel connectivity at all levels.

FIGURE 8 | Spatial variation in vegetation patterns related to slope position and fire severity relationships in dry and mesic forests in the Klamath Mountains. Topography creates contrasting conditions in fire behavior and effects; the upper third of slopes, drier aspects, and ridgetops tended to experience higher proportions of high severity fire, while valley bottoms, cooler aspects, and lower slope positions experience the lowest (Photo: Carl Skinner).

Vegetation changes related to fire exclusion and forest management have consequences for patterns of forest resilience and resistance to fire. For example, modeling experiments show that certain conifers increased their abundance and range in dry and mesic mixed forests in response to fire exclusion, and that their current distribution is misaligned with current climate and disturbance regimes (Serra-Diaz et al., 2018). Misalignment has altered stability of fire-vegetation feedbacks with potential cumulative effects on vegetation patterns at local to ecoregion levels. Altered fire-vegetation dynamics are evident in the effects of large wildfires that have burned in the Klamath and Southern Cascade Mountains over the last several decades. For example, in the Klamath Mountains, spread of high-severity fire into moist-cold Shasta red fir-*A. magnifica*, western white pine-*P. monticola*, and/or mountain hemlock-*Tsuga mertensiana* and cold forests (western white pine, Jeffrey pine, whitebark pine, foxtail pine-*P. balfouriana*, mountain hemlock, and/or curl-leaf mountain-mahogany-*Cercocarpus ledifolius*) has reduced forest resilience at locallevels, with the potential to extirpate fire-sensitive Brewer's spruce-*P. breweriana* (Skinner et al., 2018). Though there is no overall trend in total area burned at low, moderate, and high severity in large fires, there is a clear trend of increasing fire sizes along with increasing sizes of high-severity burned patches (Skinner et al., 2018). In contrast, area burned in dry and mesic forests has increased as has area burned at high severity in the Southern Cascades (Skinner and Taylor, 2018). Stand replacing fires in dry and mesic forests of the Southern Cascade and Klamath Mountains have shifted dominance from conifers to hardwoods and shrubs (Lauvaux et al., 2016; Tepley et al., 2017). High-severity reburns in flammable shrublands will likely promote long-term vegetation shifts from forests to shrublands at local, landscape and ecoregion levels (Tepley et al., 2017; Miller et al., 2018; Serra-Diaz et al., 2018; Skinner et al., 2018). Continued invasion by non-native annual grasses will further contribute to these shifts.

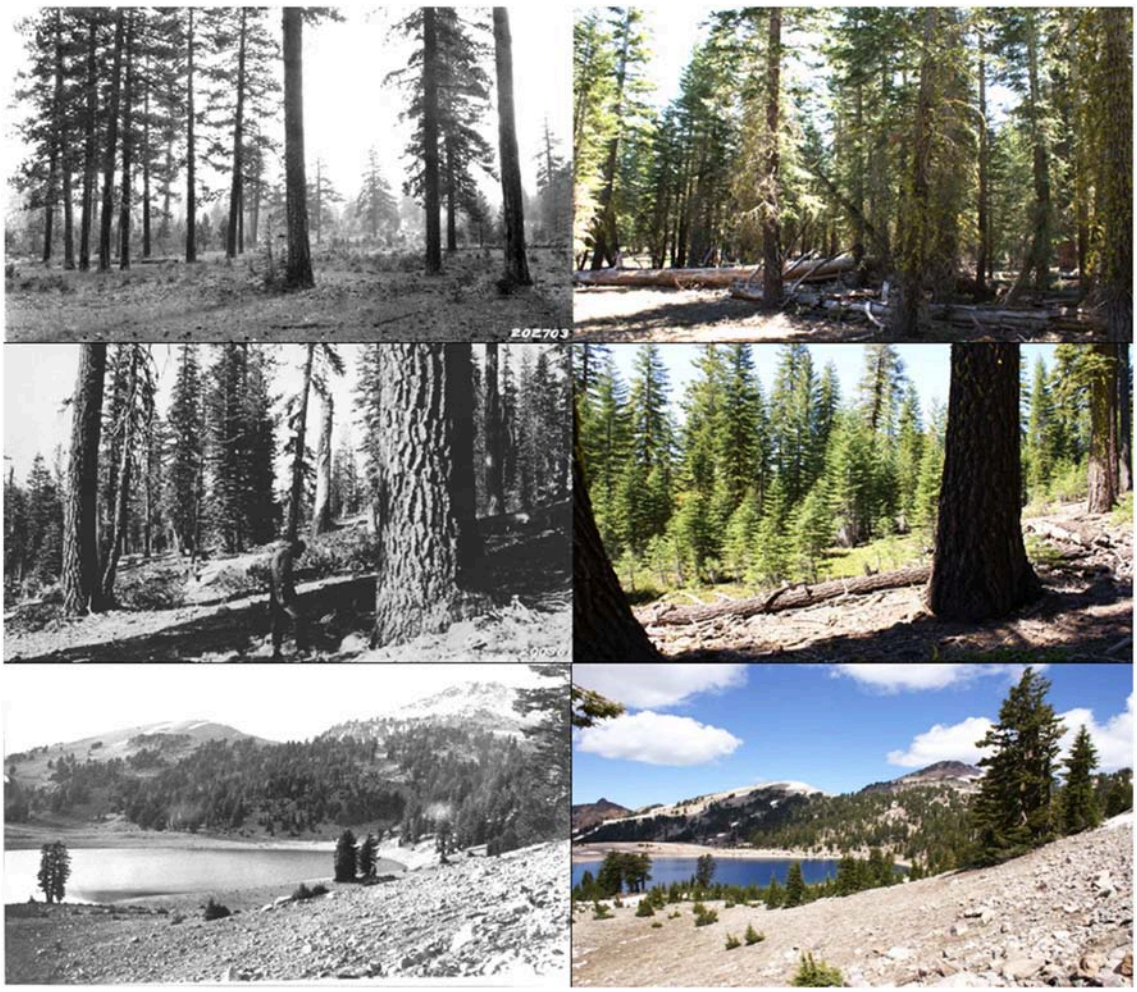

FIGURE 9 | Twentieth century forest changes in dry, mesic, and cold conifer forests in repeat photographs along an elevation-fire frequency gradient in the Southern Cascades, California. Fire regimes changed across the region after 1905 when fire suppression was implemented. Changes in tree density and species composition caused by fire suppression are more evident in dry (Top left, Weislander, 1925; Top right, Alan Taylor, 2008) and mesic (Middle left, Weislander, 1925; Middle right, Alan Taylor, 2009) forests that burned more frequently, than in cold (Bottom left, Blair, 1934; Bottom right, Alan Taylor, 2009) forests. Forests have not been logged and the photographs were taken in Lassen Volcanic National Park at referenced markers. Additional details on fire regimes and forest changes in the Southern Cascades can be found in Skinner and Taylor (2018).

While 20th-century vegetation changes are regionally significant in the Klamath Mountains, they have not overridden topography as a primary structuring influence (Estes et al., 2017; Grabinski et al., 2017). Currently, areas burned at low and moderate severity still outpace those burned at high severity, and less severely burned areas exhibit self-reinforcing behavior (Grabinski et al., 2017; Skinner et al., 2018), buffering somewhat against projected climate-induced increases in aridity, fire activity, and conifer regeneration failure (Miller et al., 2018; Serra-Diaz et al., 2018). In addition, a recent history of long-duration low- and moderate-severity wildfires reveals a region well-suited to strategically planned and intentionally managed wildfire to reduce the ongoing historical fire deficit and reduce the occurrence of high-severity fire events (Serra-Diaz et al., 2018; Skinner et al., 2018).

Sierra Nevadan Forests

Prior to Euro-American settlement, plant-available water and wildfire were primary drivers governing forest dynamics in the Sierra Nevada (SN, North et al., 2016, **Figures 2**, **6**, M261). Because 85% of annual precipitation occurs as snow in this region, water availability largely depends on winter snowpack. Overall, California experiences one of the most spatially variable precipitation regimes in the US. Spatial variability in plant-available water is influenced by landform position, soil depth and water holding capacity, and strongly influences forest type, productivity and cover (Lydersen and North, 2012). In turn, spatial variability of water availability also influences the frequency and severity of fires.

Under pre-settlement era conditions, most SN montane forests supported fire regimes characterized by frequent

low- to moderate-severity fires (every 11–16 years) in pure ponderosa, Jeffrey pine and mixed-conifer forests (ponderosa or Jeffrey pine mixed with sugar pine, incense cedar, white fir, Douglas-fir, giant sequoia-*Sequoiadendron giganteum*, black oak, canyon live oak, dogwood species-*Cornus* spp., mountain misery-*Chamaebatia foliolosa*, ceanothus-*Ceanothus* spp., and manzanitas-*Arctostaphylos* spp.). Owing to high fire frequency, extensive burning in these fire regimes was fuel- rather than climate-limited. Stand-replacing high-severity fire was a component of the historical fire regime, but only made up 5–10% of any given landscape (Safford and Stevens, 2017). Spatial patterns of stand-replacing fires consisted of many small (<4 ha), and few mid-sized patches (<100 ha, Safford and Stevens, 2017). Patterns of low-, moderate-, and high-severity fires–along with available moisture and productivity gradients–created considerable variability in landscape-level seral stage conditions (e.g., Collins et al., 2015). At the level of individual forest patches, fire and localized mortality from drought and bark beetles created heterogeneous conditions characterized by variable-sized tree clumps, individual trees, and openings, a pattern found in many frequent-fire forests (**Figure 5C**, Lydersen et al., 2013).

Variability in fuel and seral stage conditions at patch and landscape levels produced a range of vegetation structures, densities, and fuel discontinuities that made SN forests relatively resistant to large-scale mortality from wildfire and drought stress. Fire histories and tree-ring reconstructions of past droughts also suggest pre-settlement era forests were resilient to these disturbances, showing little evidence of type conversion or large-scale mortality (Swetnam and Baisan, 2003).

In the absence of fire, many modern-era SN forests now have uncharacteristically high tree densities and fuel loads (**Figure 5D**). Additionally, there is much greater surface and canopy fuel continuity evident at patch to landscape levels (Lydersen and Collins, 2018), resulting in greater potential for crownfire initiation and spread. Empirical evidence from hundreds of fires in SN forests demonstrates stand-replacing patches have become larger and less constrained by topography in recent years, and that the likelihood of tree re-establishment has diminished (Stevens et al., 2017). Beyond fire impacts, modern high-density forest conditions are susceptible to drought and bark beetles (Young et al., 2017), creating large areas of tree mortality and increased surface fuel loading.

The combination of a warming climate, drought, invasive annual grasses (in oak woodlands), increasing occurrence of extreme-fire weather events, and continued fuel accumulation is leading to more frequent and extensive fires in the SN. Climatically driven changes in wildfire could overshadow the direct effects of climate change on tree species distributions and migrations. Increased fire size, which often results in larger and more simply shaped stand-replacing patches (Stevens et al., 2017), may lead to abrupt changes in tree species compositions, reduced extent of old forest conditions, and habitats for associated species (Safford and Stevens, 2017).

Subalpine forests (including whitebark, lodgepole, and western white pine, mountain hemlock, western juniper, and Sierra juniper-*Juniperus grandis*) in the SN are largely structured by abiotic factors including snowpack depth and persistence, wind, minimum temperatures, evaporative stress and short growing season (Millar and Rundel, 2016). Higher minimum temperatures may be contributing to increased tree establishment and stand density, although there has been little change in species composition (Dolanc et al., 2013). There are few studies of historical fires in subalpine forests, however, it appears that wildfires shaped seral stage patch dynamics of local and regional landscapes, but fire was apparently not a dominant driver of within-patch dynamics. At higher elevations, rock outcrops, shallow soils, and fine-scale microclimate variability create highly diverse composition and structure (short stature krummholz cushions to 30-m tall trees), diversifying subalpine ecosystems and making them more resilient to climatic and biotic stresses. However, recent research documents increased mortality of large-diameter trees since the 1930s that is potentially associated with increased water deficits and vulnerability to insects and pathogens (Dolanc et al., 2013).

Prescribed burning and managed wildfire are effective restoration treatments for creating heterogeneity in seral stages that historically conferred resilience to many SN forests. However, these treatments are underutilized in altered SN forests, as there are numerous constraints to intentional burning (North et al., 2012). These include impacts to local communities from smoke, reduced recreational opportunities, inadequate personnel to conduct burns, liability for fire escapes, and risk-averse policies and institutions (North et al., 2015). Mechanical treatments are also effective for ecological restoration and promoting forest resilience (Collins et al., 2014). However, as with fire use, there are numerous constraints that limit the extent of treatments. Current management practices include fire suppression, which paradoxically allows occurrence of only large wildfires that escape containment during extreme fire weather conditions. Such fires generally do not restore forest resilience but instead increase the likelihood of burning again at high-severity (Coppoletta et al., 2016). Actively suppressing all wildfires except those that escape containment can entrench homogenous forest or non-forest conditions, and fails to restore the heterogeneity that supports ecosystem diversity and resilience.

Southwestern US Forests

In Southwestern (SW) US forests (**Figures 2**, **6**, M313, 313, M331), species composition, structure, and spatial distribution are shaped by climate influences on wildfire regimes and forest productivity. Climate affects the spatial distribution of forests through synoptic (broad-scale) regeneration, growth, mortality, and disturbance events. Topographic gradients in temperature, solar radiation and water availability increase the spatial complexity of forest structure and composition (O'Connor et al., 2017). Regionally, area burned is synchronized with wet-dry phases of the El Niño-Southern Oscillation (ENSO). Increases in area burned are partially driven by increased plant growth during wetter years, which increases landscape connectivity of fine fuels (Swetnam et al., 2016). Within-year fire season length varies as a function of time between winter snowmelt and the summer monsoon (Westerling, 2016). Low- to mid-elevation forests are

available to burn each year, whereas cool, higher-elevation forest availability to burn is driven by snowpack longevity and extreme fire weather.

Southwestern forests are continuously shaped by interactions among climate-related stressors, including fire, drought, and insect outbreaks (Allen, 2007; Williams et al., 2013). Climatic conditions and combined natural and human-caused ignitions resulted in fire frequency generally varying as a function of elevation over the historical period (Hurteau et al., 2014; O'Connor et al., 2017). In low- and mid-elevation forests, dry lightning preceding summer rains and aboriginal fire use provided abundant ignitions (Swetnam et al., 2016); resulting fires created heterogeneous forest structures at patch to landscape levels. At higher elevations, low fire frequency and faster buildup of high fuel loads resulted in larger moderate- and high-severity fire patches, which created complex seral stage patterns (Margolis et al., 2011).

At low and mid elevations, dry ponderosa pine and dry mixed-conifer forests (ponderosa pine with Douglas-fir, white fir, occasionally with southwestern white pine, limber pine, often with quaking aspen, and/or Gambel oak) historically exhibited mean fire return intervals (FRIs)–ranging from 2 to 16 year–that maintained relatively open-canopy conditions with well-developed understory plant communities (Hurteau et al., 2014). Frequent fires and resultant open-canopy structures (**Figure 5C**) enabled these forests to resist high-severity fire, while higher-elevation mesic mixed-conifer forests (Douglas-fir with quaking aspen, white fir, southwestern white pine-*Pinus strobiformis*, and blue spruce-*P. pungens*), with mean FRIs of 3–25 year, experienced low- and mixed-severity fires (Hurteau et al., 2014). Spruce-fir forests (Engelmann spruce, occasionally with blue spruce, corkbark subalpine fir-*Abies lasiocarpa* var. *arizonica*, Douglas-fir, white fir, limber pine, and bristlecone pine-*Pinus aristata*) at the highest elevations typically experienced infrequent stand-replacing fires (Margolis et al., 2011; O'Connor et al., 2017).

By ca. 1900, land-use change and fire suppression had interrupted fire regimes across the Southwest, followed by episodic climate conditions favoring tree establishment and growth (Covington and Moore, 1994). Over the 20th century, these factors combined to increase forest area, density, layering, and surface fuel accumulations, resulting in greater homogeneity of highly-connected forest with high fuel loads. This widespread structural homogenization has made SW forests more susceptible to high-severity fire at patch, landscape, and ecoregion levels (Allen, 2007, 2014). Also, regional drought since ∼1998 and increasing temperatures from ongoing climate change are exacerbating tree mortality (Williams et al., 2013). For example, the area burned by wildfire has increased by 1,200% over the past 40 years as temperature has increased (Westerling, 2016). Increasingly large patches of stand-replacing fire are driving these homogenous forests toward non-forest conditions as conifer seed sources become limited and grasslands (including invasive annual grasses) and shrublands expand. In addition, densified forests that have not recently experienced fire are also widely affected by drought-induced growth stress and tree mortality (Williams et al., 2013). The combined effects of higher temperatures, reduced precipitation, and larger patches of high-severity fire are limiting postfire conifer establishment (Shive et al., 2013; Hurteau et al., 2014; Ouzts et al., 2015; Coop et al., 2016). The interactions among climate and land-use changes that drove widespread forest structural homogenization have set up SW forests for significant spatial contraction after fire (Allen, 2014).

Prior to fire-exclusion, forest structural heterogeneity was central to maintaining ponderosa pine, mixed-conifer, and spruce-fir forest resilience and resistance to wildfires. Forest densification and homogenization via fire-exclusion–coupled with ongoing climate change–has greatly reduced resistance to high-severity fire in many SW ponderosa pine, mixed-conifer, and even spruce-fir forests (Allen, 2014; O'Connor et al., 2017). Empirical evidence suggests that lower total precipitation and higher variation in interannual precipitation in low-elevation forests has increased the likelihood of transition from forest to non-forest conditions (Hurteau et al., 2014). With increasing large-fire frequency (Westerling, 2016), we can expect reduced postfire forest resilience driven by reduced conifer seed-rain and drier climate conditions (Coop et al., 2016).

Both the ecological consequences and benefits of fire as a function of fire-severity have long been recognized in the SW US (Swetnam et al., 2016). Reconstructions of historical fire-maintained forest structure, especially in ponderosa pine, have informed many current management practices that seek to increase structural heterogeneity through mechanical thinning and reintroduction of surface fire. However, similar to the challenges faced in other fire-prone regions, treatment costs, public support, and topographic constraints have limited the pace and scale of that re-introduction. In remote backcountry areas (e.g., the Gila Wilderness), management of natural fire ignitions to maintain this important process has been in place for decades, and such "wildland fire use" is becoming increasingly common region-wide. Recent wilderness research re-affirms that landscapes with more characteristic fire regimes are better able to self-regulate fire size and severity, even as the climate changes (Parks et al., 2014, 2015).

Questions remain regarding what can be gained by restoring fire to some of the driest SW forests. As temperatures continue to rise, and interannual precipitation variability remains high, the potential exists for ongoing, widespread tree mortality—a phenomenon that has occurred during prior hot droughts (Allen, 2007; Williams et al., 2013). Further, increasingly large high-severity fires can trigger vegetation shifts in concert with ongoing climate change (Allen, 2014; Coop et al., 2016; Parks et al., 2019). The societal implications of large, high-severity fires are already being realized in terms of impacts on water supply (Smith et al., 2011), carbon sequestration, and air quality; more managed fire can ameliorate all of these impacts (Hurteau et al., 2014). Yet, it remains to be seen how restoring historical forest structures and frequent-fire regimes to these ecosystems will affect projected rates of climate-induced forest loss from growing regional drought stress (Williams et al., 2013), and how Southwestern topographic variability may moderate regional climate change and create tree refugia in cooler and wetter

sites. Regardless of these uncertainties, restoring forest structural heterogeneity provides a strong bet-hedging strategy against ongoing climate-change impacts.

Northern Baja California Forests (Mexico)

The Baja Peninsula of California (**Figures 2**, **6**, M262, M263) is traversed by the Peninsular Ranges, a north-south trending backbone of westward-tilted fault blocks that stretch from southern California to Cabo San Lucas. In the northern part of the Mexican Peninsular Range reside the Sierra Juarez (SJ) and Sierra de San Pedro Mártir (SSPM) conifer forests (Bullock, 1999). The SJ and SSPM forests are mainly underlain by granitic lithologies, which yield well-drained soils with limited water holding capacity (Stephens and Gill, 2005; Fry et al., 2018). To the west, the Sierras slope gently toward the Pacific coast, on the east they are bounded by steep, tall escarpments that abruptly drop to the Sonoran desert. Climate in the northern Baja Mountains is Mediterranean, with a stronger summertime monsoonal influence than is experienced in similar Sierra Nevada (SN) sites farther north. Winters are cool and moist, summers are warm and dry. In the SSPM, annual precipitation ranges from 400 to 700 mm, mostly falling as winter snow, however, 10–20% of annual precipitation falls as rain in summer due to the North American monsoonal influence (Minnich et al., 2000; Skinner et al., 2008; Dunbar-Irwin and Safford, 2016).

The Kumiai, Pai Pai and Kiliwas aboriginal cultures inhabited northern and central Baja California before the arrival of European settlers (Shipek, 1993); a nomadic lifestyle permitted them to follow resource availability with the changing seasons. According to Barbour et al. (1993), fires were intentionally set by aboriginals to open shrublands for hunting and passage, and to increase grass production. In the summer, Kiliwas and Pai Pai moved to high-elevation meadows in the Peninsular Ranges to hunt and collect seeds, but snowy winters did not permit year-round habitation (Meigs, 1935; as cited in Stephens et al., 2003). After the founding of the mission of San Pedro Mártir in 1794, livestock became a seasonal presence in the conifer forests and montane meadows. From 1924 to 1965 there were 6,000 sheep in the SSPM, but sheep have been almost entirely replaced by cattle today (Stephens et al., 2003). Livestock use of national park lands is technically prohibited in Mexico, but hundreds of cattle from local *ejidos* (communal farmlands or cooperatives) continue to use SSPM ranges for summer forage.

The Peninsular Ranges in the northern Baja California (north of 30° latitude) support conifer forests above 1,500 m in the SJ, and above 1,800 m in the SSPM. The SJ is dominated by open forests and savannas of Parry pinyon and Jeffrey pine, often with an understory of sagebrush-*Artemisia* spp. Forests of the SSPM occur at higher elevations (up to 3,096 m at Picacho del Diablo) and support most of the tree species that are typical of southern California yellow pine (syn. Jeffrey pine) and mixed-conifer (YPMC) forests, including Jeffrey pine, sugar pine, white fir, lodgepole pine, incense cedar, quaking aspen, and canyon live oak. A few local and regional endemic tree species also occur, such as peninsular oak-*Q. peninsularis*, which fills a niche similar to black oak in southern California, and San Pedro Martír cypress-*Cupressus montana*. Forest understories are dominated by buckbrush, manzanita, seer's sage-*Salvia divinorum*, beardtongue-*Penstemon* spp., wildmint-*Monardella* spp., and needlegrass species-*Stipa* spp.).

Although the general environment of the SSPM is highly similar to YPMC forests of the San Jacinto Mountains or the east slopes of the SN (Dunbar-Irwin and Safford, 2016), their management histories differ markedly. Whereas, most YPMC forests in the eastern SN were extensively logged during the late 19th and 20th centuries, the SSPM has only experienced minor levels of timber harvesting in the lower elevations. Perhaps more importantly, fire suppression activities in the SSPM began only 30 year ago, compared with over a century of fire suppression in California (Stephens et al., 2003). Considering both lower productivity and growth rates and relatively low impacts of past forest management, forest structure and composition in the SSPM are much less altered by past management than the highly similar SN forests (Fry et al., 2014). As a result, the SSPM is considered an important living reference forest for restoration of SN dry YPMC forests (Stephens and Fulé, 2005; van Wagtendonk and Fites-Kaufman, 2006; Dunbar-Irwin and Safford, 2016). Resilience and resistance mechanisms are largely intact in these forests owing to the relative absence of timber harvest, and limited influence of fire suppression activities.

Wildfire burn severity was recently evaluated via remote sensing techniques in the SSPM for the period 1984 to 2010. Results were then compared with similar YPMC forests in the SN, for approximately the same period (**Figure 10**). SSPM forests displayed a much lower fraction of high-severity burned area (3–5 vs. 30%) than those of the SN (Rivera-Huerta et al., 2016). Historical reconstructions, modern forest reference data from SSPM, and remote sensing data all suggest that prior to Euro-American settlement, YPMC forests in the SN of California also experienced a primarily high frequency, low-severity fire regime, with high-severity burning seldom exceeding 5–10% of the area (Safford and Stevens, 2017). **Figure 10** shows the dramatic differences in modern burn severity between the SSPM and the SN. Differences are driven primarily by different forest and fire management histories, with extensive logging and a century of fire suppression the SN leading to dense, layered, homogeneous, and fuels-rich forests dominated by less commercially-valuable fire-intolerant trees (Safford and Stevens, 2017; van Wagtendonk and Fites-Kaufman, 2006).

Past management has not only increased fire severity in YPMC forests, it has also increased susceptibility to drought and bark beetle induced mortality that has killed >130 million trees in the southern SN since 2015; similar mortality has not occurred in the more resilient SSPM forests (Stephens et al., 2018). Conservation of the SSPM is a high priority as it is one of the few large landscapes left in the Northern Hemisphere where forests adapted to frequent fire are still largely intact. Going forward, management that allows the continued influence of frequent fires will maintain SSPM forest in a resilient condition, and allow them to adapt gradually to changing climatic conditions.

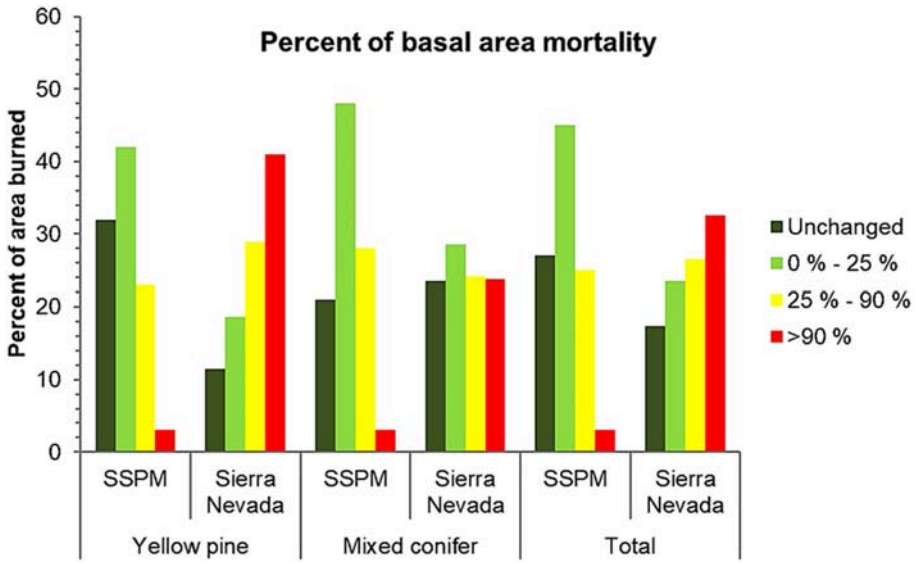

FIGURE 10 | Comparison of mean fire severity distributions in the Sierra de San Pedro Mártir (SSPM) National Park, Mexico, and the Central Sierra Nevada of California for the period 1984–2010. Sierra Nevada data from J.D. Miller, USDA Forest Service, McClellan, California. Darker green bars represent 0% change, light green bars represent low-severity fire (0–25% change), yellow bars represent moderate-severity fire (25–90% change), and red bars represent high-severity fire (> 90%change, Rivera-Huerta et al., 2016). Yellow pine is another name for Jeffrey pine.

SYNTHESIS

Across western North American ecoregions, we find that a strong core of emergent properties historically conferred forest resilience and resistance to disturbances and climatic changes. We synthesize them here.

Scale-Dependent Spatial Controls Drive Wildfire Behavior and Effects

Wildfires were historically influenced by broad-, meso-, and fine-scale factors (Peterson et al., 1998; Moritz et al., 2011). Top-down broad-scale factors included a wide range of climatic, weather, geologic or geomorphic events. Bottom-up factors included fine-scale surface fuel loading, microsite conditions, tree density, endemic insect and disease incidence and severity, topography, and local continuity of tree canopies, ladder and understory fuels. Meso-scale factors of local landscapes included patchworks of forest and non-forest, fuel and successional conditions, productivity and topoedaphic settings. These broad-, meso-, and fine-scale factors together influenced biotic and wildfire conditions. Under more extreme annual climate and fire weather conditions, top-down factors drove occurrence and effects of the largest fires. Under the most moderate climate and fire weather conditions, bottom up factors spatially controlled the sizes and effects of smaller fires. Fires in the middle range of sizes were likely driven by a tug-o-war among top-down and bottom-up factors interacting under less than extreme climate and fire weather conditions. Because forcing by top-down drivers can be so highly influential, we suggest that forest resilience and resistance have always been mutable rather than static system properties (Millar and Woolfenden, 1999). Hence, the study and characterization of historical ecology over varying climatic regions and periods is critical to understanding the components and configurations of resilient ecosystems (Swetnam et al., 1999).

Cross-Connections Between Broad- and Meso-Scale Landscapes Mediate Fire Behavior and Effects

From our survey of ecoregions, we see that historical wildfires influenced and were influenced by cross-connections between broad physiognomic patchworks of non-forest and a mix of forest successional conditions (*sensu* Wu and Loucks, 1995). Non-forest types had surface fuels—typically grasses, herbs, and dry or moist site shrubs—that often supported, and were supported by, moderate or high frequency fires. Historically, ignitions often spread quickly when they made contact with this non-forest patchwork, and owing to flashy fuel conditions, fires spread relatively quickly, but flame lengths and fireline intensity were fairly low. The primary fire behavior was accordingly surface rather than crownfire in the intermingled patches of dry and moist forest. Non-forest patches were not restricted to low productivity sites; some occurred in topoedaphic settings that could readily support forest. Thus, the potential extent of forest area based on climate and environmental settings alone (i.e., the carrying capacity) was seldom realized historically (Bond and Keeley, 2005). Multi-scale feedbacks with wildfire were necessary for creating and maintaining these patchworks. Characterizing the natural variability of these non-forest and pre-forest patchworks in each unique ecoregion and understanding the mechanisms responsible for that variability is a key to understanding and restoring broad landscape resistance to severe wildfires, and resilience in the face of climatic changes.

Similarly, forest successional patches in drier environmental settings were open canopy with flashy surface fuels that favored surface fire spread, while those in cool-moist settings had more complexly layered fuels and instead favored mixed surface and crownfires, or predominantly crownfires. Fire controlled the successional patchwork and maintained much of the landscape in open-canopy conditions, which reduced sensitivity of trees to drought (Voelker et al., 2019). During cool-moist climatic periods of lower than average fire frequency, tree densities would increase and patches of nearby forest or woodland would expand, encroaching on and reclaiming areas of grass- and/or shrubland. However, during hot-dry climatic periods with elevated fire frequency and severity, grass, shrub, and woodland areas would again expand (e.g., see Beaty and Taylor, 2009), often in new locations, and tree densities would decline. Restoring this kind of natural spatial and temporal variation in forest successional patchworks is fundamental to restoring forest resilience (Moore et al., 1999; Keane et al., 2009).

Cross-Connections Between Meso- and Fine-Scale Landscapes Influence Fire Frequency and Severity

Across the surveyed ecoregions, we also found cross-connections and interactions whereby wildfires historically shaped and were shaped by fine-grained vegetation patterns within and among patches (Harvey et al., 2017). Fire interacted with patches of intermingled non-forest, dry, moist, and cold forests, which maintained high spatial variability in fire frequency and severity and resulted in a multi-level mosaic of seral stages and associated fuelbeds (Prichard et al., 2017). For example, frequent surface fires would spread from dry forests into adjacent moist or cold forest patches, thereby maintaining lower surface fuel loads and structures than otherwise might occur with that forest type. These spatial interactions explain the presence of open-grown lodgepole pine trees with multiple fire scars, and historical subalpine ribbon forests interspersed with wet and dry meadows (**Figure 11**). Historical forest successional landscapes were seldom at carrying capacity with regard to forested area or density as a consequence of disturbance mediated feedbacks operating at meso- and fine-scales.

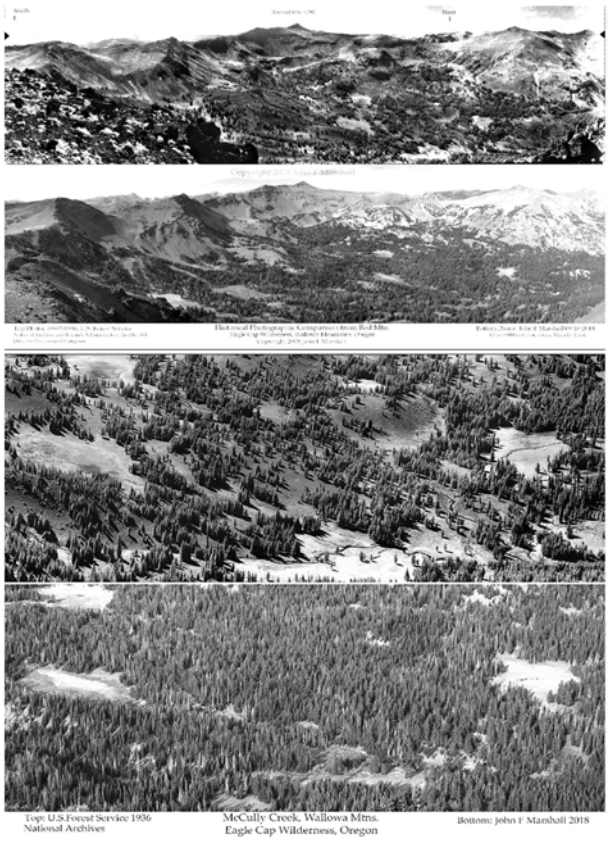

FIGURE 11 | *Top pair,* Panoramic (120°) comparison of high elevation (2,400–2,700 m) cold forests of the McCully Creek basin. Top photo is from 1936, from the William Osborne collection, looking WSW to Aneroid Mountain from the top of Red Mountain. Forests are mixed lodgepole pine, subalpine fir, and Engelmann spruce. Notice that the headwaters of this basin was historically dominated by dry and wet meadows with interspersed ribbons of forest. Bottom photo of the pair is from 2018, taken by John Marshall. Notice the infilling of forest and decline in meadow area. *Bottom pair,* close-up of a portion of the top photo pair. The scene is McCully Creek. Notice in the top photo, that size classes of open-grown trees are variable indicating that meadow invasion/expansion is dynamic in the interval between fires. In the bottom photo, widespread bark beetle mortality is indicated by gray lodgepole pine and spruce snags, which are absent in the top photo. Loss of meadow is conspicuous in the bottom photo.

Species Traits and Adaptations Drive Patch Structure, Composition, and Response to Disturbances

Within patches, physiological traits and adaptations of species such as serotiny, thick bark, and reproduction strategies were critical not only to species persistence, but to the maintenance of characteristic vegetation structure and composition, as well as fire severity. Medium- and large-sized ponderosa and Jeffrey pine, western larch, and Douglas-fir displayed elevated crown bases that prevented fire from climbing into the canopy, and thick bark that insulated them from most basal scorching. Shrubs resprouted from deep root systems or via seeds long buried in soils. Native grasses were fire-adapted and some formed sods, which were available to reburn within a year. Bunchgrasses grew in individual tufts and tussocks, which provided fine-scale fuel discontinuities while also making them resistant to fire caused mortality. Patch-level structures such as clumped and gapped tree distributions were also supported by recurrent fires (Larson and Churchill, 2012; Churchill et al., 2013; Lydersen et al., 2013). Clump and gap sizes varied predictably with species-level traits including seed dispersal distances and in-filling rates, and with patchy tree mortality driven by surface and ladder fuels (**Figure 5C**). Restoring more typical tree clump and gap size variation is key to restoring patch-level resistance to severe wildfires, and to adapting patches to coming climatic changes (Pawlikowski et al., 2019), particularly in dry and moist mixed conifer forests.

Climate Change Will Reduce Forest Area and Density

Cross-connections between broad-, meso-, and fine-scale landscapes offer clues to expected warming and drying of western North America and its consequences for fire and vegetation dynamics (Keane et al., 2013; Kitzberger et al., 2017; Davis et al., 2018). Increasing moisture deficits will likely contribute to continued declines in tree vigor and forest area to levels that are even lower than occurred historically. As non-forest area grows, area burned will likely increase across flashy fuel-connected landscapes. This may have the effect of increasing fire frequency not only in dry forests, but also in some moist and cold forests, especially as they intermix with dry forests on topographically diverse landscapes. In rugged terrain, topography will continue to influence fire size and severity (Povak et al., 2018), but with continued warming, we may see an erosion of topographic controls. Increased fire frequency will reduce canopy cover and tree density while favoring plant species with traits that allow them to survive or colonize quickly following fire. These trends may ultimately increase the amount of low- and moderate-severity fire compared to what historically was associated with each forest type, thus redefining their characteristic feedbacks and the associated forest and non-forest successional conditions.

CONCLUSIONS

Resilience mechanisms are strikingly similar across a wide range of western North American environmental conditions. Resilience arises through incremental and sometimes punctuated adaptations to the prevailing climate at each level of organization. Adaptations occur at species- and community-levels via physiological and life history traits, and through physiognomic patterning at the ecoregion-level. During periods of modest climatic variation, multi-level patterns support a system that appears to be stable, while not truly stable (metastability). When fueled by extreme disturbance or climatic events, this apparent stability can mutate, changing the dominance and distribution of landscape conditions at all levels. We showed clear evidence that such changes in western North American forests have resulted from human, disturbance, and climatic influences.

Broad-scale and abrupt changes in landscape structure and organization can be difficult for native plants, animals, and human communities to withstand (Liu et al., 2007; Spies et al., 2014). Accordingly, a task for current era managers is to *manage for the changes, with uncertainty clearly in mind.* Promoting forest resilience or resistance to wildfires and other disturbances will require planning on an uncertain amount of unbridled and ongoing disturbance. It will necessitate being mindful and inclusive of species-level traits; characteristic patch-level tree clump and gap distributions, tree sizes, densities, and canopy layers; meso-scale seral stage and fuelbed heterogeneity; and broad-scale forest and non-forest patchworks. Intentionally fostering ecosystems that can reside deeper in the figurative resistance basin, or that have a broad resilience basin of attraction to move around in, will lessen their vulnerability to coming climatic and wildfire regime changes. This may require pre-emptively adapting landscapes in areas with anticipated future water deficit, before abrupt changes occur from disturbance- or drought-related mortality events. Examples of preparing landscapes for the coming wildfire and climatic regime changes include reducing forest area, expanding woodland or grassland area, reducing canopy cover and layering, and increasing the areal extent of large trees of fire-tolerant species. In these ways, managers can also better prepare human communities for future uncertainty by reducing the likelihood of abrupt broad-scale changes.

We are doubtful that purposeful and pro-active land management will succeed without active engagement of human communities that depend on these landscapes (Fischer et al., 2016). Social science research finds high levels of public support for some pro-active forest management, such as thinning and prescribed-burning on public lands with a high fire risk (Burns and Cheng, 2007; McCaffrey et al., 2013). However, it is unknown whether such support exists for mitigating other risks to forests, such as large-scale bark beetle outbreaks (Flint et al., 2009; McFarlane et al., 2012). Evidence points to public mistrust of some forest managers, and a lack of agreement about the conditions conferring large landscape vulnerability and the benefits and methods of well-timed proactive treatments (Spies et al., 2018b). Clearly more work is needed to understand the nature of interdependence among social-ecological communities and their governance before managers can reliably motivate the kind of change that results in the "greatest good for the greatest number."

Managing for resilient forest landscapes depends on scale and social values. It involves human community changes and adaptations that are concordant with the ecosystems they depend on. It entails exploiting factors and mechanisms that drive dynamics at each level to adapt landscapes, species, and human communities to climate change, while maintaining core ecosystem functions, processes, and services. Finally, it compels us to prioritize management that incorporates ongoing disturbances and anticipated effects of climatic changes, and supports dynamically shifting patchworks of forest and non-forest. Doing so could make these shifting forest conditions and wildfire regimes less disruptive to individuals and society.

AUTHOR CONTRIBUTIONS

PFH, CM, AL, NP, CA, MH, AT, PEH, SJP, VK, and DC: contributed to the conception and design of the study. PFH: wrote the first draft of the manuscript. All authors wrote sections of the manuscript and contributed to manuscript revision, read and approved the submitted version.

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REVIEW
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Operationalizing Ecological Resilience Concepts for Managing Species and Ecosystems at Risk

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This review provides an overview and integration of the use of resilience concepts to guide natural resources management actions. We emphasize ecosystems and landscapes and provide examples of the use of these concepts from empirical research in applied ecology. We begin with a discussion of definitions and concepts of ecological resilience and related terms that are applicable to management. We suggest that a resilience-based framework for management facilitates regional planning by providing the ability to locate management actions where they will have the greatest benefits and determine effective management strategies. We review the six key components of a resilience-based framework, beginning with managing for adaptive capacity and selecting an appropriate spatial extent and grain. Critical elements include developing an understanding of the factors influencing the general and ecological resilience of ecosystems and landscapes, the landscape context and spatial resilience, pattern and process interactions and their variability, and relationships among ecological and spatial resilience and the capacity to support habitats and species. We suggest that a spatially explicit approach, which couples geospatial information on general and spatial resilience to disturbance with information on resources, habitats, or species, provides the foundation for resilience-based management. We provide a case study from the sagebrush biome that illustrates the use of geospatial information on ecological and spatial resilience for prioritizing management actions and determine effective strategies.

Keywords: ecological resilience, spatial resilience, landscape context, ecosystems, natural resources management, restoration, conservation, management framework

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INTRODUCTION

Globally ecosystems are changing at an unprecedented rate largely due to human impacts, including land development and use, pollutants, invasive species, altered disturbance regimes, increasing CO_2, and climate change. Changes in species distributions and the emergence of novel ecosystem states increasingly challenge our capacity to manage for biodiversity, ecosystem functioning, and human well-being (IPCC, 2014; Pecl et al., 2017). Effective management of ecosystems in this era of rapid change requires an understanding of an ecosystem's response not only to these stressors and disturbances but also to management actions. Clear formulation and application of ecological resilience concepts can provide the basis for managing

ecosystems to enhance their capacity to cope with stressors and disturbances and help guide them through periods of reorganization. Periods of reorganization provide both crisis and opportunity, and management during these periods is critical. Ecological resilience concepts (see **Table 1** for definitions) can provide the basis for increasing the capacity of systems to absorb, persist, and adapt to inevitable and unpredictable change (Curtin and Parker, 2014), and for taking advantage of management opportunities to transform systems to more desirable states.

Operationalizing ecological resilience concepts for management has been difficult because a framework for evaluating how ecosystem responses to disturbances and stressors vary over large heterogeneous landscapes and how this variation is related to ecological resilience has not been well developed or translated for the management community. Applying these concepts at scales relevant to management is becoming increasingly important as the scale and magnitude of ecosystem change increase. To date, much of the literature on ecological resilience has focused on theory, definitions, and broad conceptualizations regarding the application of resilience concepts (e.g., Gunderson, 2000; Folke et al., 2004, 2010; Walker et al., 2004; Folke, 2006; Gunderson et al., 2010). Much of the research has focused on the importance of species diversity and species functional attributes in affecting responses to stress and disturbance at fairly small (local) scales (e.g., Angeler and Allen, 2016; Baho et al., 2017; cf. Pope et al., 2014; Roberts et al., 2018).

Recently, two applications of ecological resilience have come to the forefront and are being used at scales relevant to management. Assessments of general resilience, or the broad ability of systems to maintain fundamental structures, processes, and functioning following disturbances (after Folke et al., 2010), are being used to evaluate differences in the responses of the ecosystems that comprise landscapes and identify which ecosystems are likely to exhibit critical transitions to alternative states (e.g., Hirota et al., 2011; Brooks et al., 2016; Levine et al., 2016). These assessments are based on an understanding of the relationships among an ecosystem's environmental characteristics, attributes and processes, and responses to stressors and disturbances (Chambers et al., 2014a,c, 2017a,b). Assessments of spatial resilience, or how spatial attributes, processes, and feedbacks vary over space and time in response to disturbances and affect the resilience of ecosystems (after Allen et al., 2016), are being used to evaluate the capacity of landscapes to support ecosystems and biodiversity over time. These assessments are based on an understanding of the changes in landscape composition and configuration in response to disturbances and the effects on ecosystems and species (Frair et al., 2008; Keane et al., 2009; Olds et al., 2012; Hessburg et al., 2013; McIntyre et al., 2014; Tambosi et al., 2014; Rappaport et al., 2015). The concept of spatial regimes (Sundstrom et al., 2017; Allen et al., 2018; Roberts et al., 2018) represents a novel integration of space into traditional regime shift and early warning research. Developing an understanding of both general and spatial resilience has become more tractable over time because of the rapid development of the field of landscape ecology and the number of tools and models now available (Turner, 1989; Wu and Loucks, 1995; McKenzie et al., 2011).

Managing for ecological resilience necessarily requires a multiscale approach because of the nested, hierarchical nature of complex systems (panarchy; Holling, 1973; Wu and Loucks, 1995; Allen et al., 2016). Incorporating larger scales provides

TABLE 1 | Common definitions for understanding ecological resilience concepts.

Adaptive capacity – The ability of a system to maintain critical functions and processes during changing and/or novel environmental conditions (Angeler and Allen, 2016).

Alternate states – An alternative configuration of a system that differs in terms of species composition and abundance, patterns, processes, and feedbacks. Stable states are alternative states that are separated by thresholds (Lewontin, 1969).

Ecological resilience – A measure of the amount of change needed to change an ecosystem from one set of processes and structures to a different set of processes and structures, or the amount of disturbance that a system can withstand before it shifts into a new regime or alternative stable state (Holling, 1973). In applied ecology, ecological resilience is also used as a measure of the capacity of an ecosystem to regain its fundamental structure, processes, and functioning (or remain largely unchanged) despite stresses, disturbances, or invasive species (e.g., Hirota et al., 2011; Chambers et al., 2014a; Pope et al., 2014; Seidl et al., 2016).

General resilience – A general and generic property of systems that describes the broad ability of a system to regain fundamental structures, processes, and functioning following disturbances (based on Folke et al., 2010). General resilience is a function of environmental characteristics and ecosystem attributes and processes and is a useful concept for describing differences among ecosystems at landscape scales.

Resistance – Capacity of an ecosystem to retain its fundamental structure, processes and functioning (or remain largely unchanged) despite stresses, disturbances, or invasive species (Folke et al., 2004).

Resistance to invasive species – The biotic and biotic attributes and ecological processes of an ecosystem that limit the population growth of an invading species (D'Antonio and Thomsen, 2004).

Regime shifts – Changes in the processes and feedbacks that confer dynamic structure to a given state of a system. A change in the regime of a system may result in a state change, depending on the type and magnitude of regime change and initial state of the system.

Spatial resilience – A measure of how spatial attributes, processes, and feedbacks vary over space and time in response to disturbances and affect the resilience of ecosystems (based on Allen et al., 2016). In a landscape context, spatial resilience is a function of landscape composition and configuration.

State-and-transition model – A method to organize and communicate complex information about the relationships among vegetation, soil, animals, hydrology, disturbances (fire, lack of fire, herbivory, drought, unusually wet periods, insects, and disease), and management actions on an ecological site (Caudle et al., 2013).

Threshold – The point at which there is an abrupt change in ecosystem states, or where small changes in one or more external conditions produce large and persistent responses in an ecosystem (Allen et al., 2016). When an ecosystem crosses a threshold or tipping point, its capacity to adapt to and cope with disturbances has been exhausted, and it abruptly reorganizes into a new regime with new structures, functions, and processes.

Transitions – The loss of state resilience due to abiotic or biotic variables or events, acting independently or in combination, that results in shifts between states. Transitions are often triggered by disturbances, including natural events (climatic events or fire) and/or management actions (grazing, prescribed fire, fire suppression). They can occur quickly as in the case of catastrophic events like fire or flood, or over a long period of time as in the case of a gradual shift in climate patterns or repeated stressors like frequent fires (Caudle et al., 2013).

the basis for directing limited management resources to those areas on the landscape where they are likely to have the greatest benefit (Holl and Aide, 2011; Allen et al., 2016; Chambers et al., 2017c). Restoration efforts or conservation measures for individual species or small areas within large landscapes are often applied with the best of intentions but are unlikely to succeed in the long-term if they do not consider the larger environmental context, pattern and process interactions, and essential ecosystem elements, such as biodiversity, habitat connectivity, and capacity to supply ecosystem services over time.

Here, we focus on the use of resilience concepts to guide natural resources management actions. We emphasize ecosystems and landscapes as focal levels of assessment and provide examples of the use of these concepts from empirical research in natural resources management. We begin by discussing definitions and concepts of ecological resilience and related terms that are applicable to management. We suggest that a resilience-based approach to management facilitates regional planning by providing the ability to locate management actions where they will have the greatest benefits. We review the six key components of a resilience-based approach, beginning with managing for adaptive capacity and selecting an appropriate spatial extent and grain. Critical elements include developing an understanding of the factors influencing the general and ecological resilience of ecosystems and landscapes, the landscape context and spatial resilience, pattern and process interactions and their variability, and relationships among ecological and spatial resilience and the capacity to support habitats and species. We suggest that a spatially explicit approach, which couples geospatial information on general and spatial resilience to disturbance with information on resources, habitats, or species, provides the foundation for prioritizing areas for management actions. We provide a simple decision support tool that illustrates the use of geospatial information on general and spatial resilience for prioritizing management actions and determining effective strategies.

DEFINITIONS

Definitions and concepts related to ecological resilience (**Table 1**) have been widely adapted in applied ecology, including conservation biology (Curtin and Parker, 2014), restoration ecology (Bradshaw and Chadwick, 1980; Aronson et al., 1993; Suding et al., 2004), range science (Westoby et al., 1989; Laycock, 1991; Briske et al., 2005, 2008), wildfire science (Moritz et al., 2011), fisheries ecology (Pope et al., 2014), and geomorphology (Brunsden and Thornes, 1979; Downs and Gregory, 1993; Phillips, 2009). In applied ecology, ecological resilience is often interpreted as a measure of the potential of a system to recover to a desired state, i.e., the capacity of an ecosystem to regain characteristic processes, structures, functions, and feedbacks following disturbance or management actions (e.g., Chambers et al., 2014a; Pope et al., 2014; Trombore et al., 2015; Seidl et al., 2016). However, it is important to recognize that ecological resilience also applies to undesirable states (Zelmer and Gunderson, 2009), which may be highly resilient to management actions designed to return them to an original state, or transform them into more desirable states. In this context, resilience management entails (1) actively maintaining or enhancing ecological processes, structural and functional characteristics, and feedbacks of intact or desirable states, (2) eroding the resilience of undesirable states and fostering transitions to more desirable alternative states, and (3) increasing the capacity of systems to cope with new or altered disturbance regimes and climate change (e.g., Pope et al., 2014).

Although many of the resilience definitions and concepts used in applied ecology were derived from Holling's (1973) original papers and resilience science, others have evolved independently. For example, in geomorphology, landform sensitivity is defined similarly to ecological resilience. It is the (1) the propensity of a system to change as governed by a set of driving and resisting forces, and (2) the capacity of the system to absorb or resist the effects of the disturbance (Downs and Gregory, 1993). Other definitions have been derived as new ecosystem threats and disciplines have emerged. For example, in invasive species ecology, resistance to invasion is defined as the abiotic and biotic attributes and ecological processes of an ecosystem that limit the population growth of an invading species (D'Antonio and Thomsen, 2004).

Confusion regarding use of the term resilience in applied ecology can arise because in disciplines such as disaster management, the term resilience is often used as a process, as in enhancing resilience. This use of the term is normative and should be avoided. In various other disciplines, like engineering and medicine, resilience is defined as a rate of recovery. Measuring rates of recovery is straight forward, and often desirable, but fails when a system is non-stationary and where thresholds and alternative states occur (Angeler and Allen, 2016). Striving for consistent use of the terms can help promote a common understanding of ecological resilience and facilitate its application to management. Recognizing the similarities and resolving the differences among the use of the definitions and concepts can help foster the necessary interdisciplinary collaboration for effective management.

RESILIENCE CONCEPTS

States, Transitions, and Thresholds

Following disturbances or management actions, ecosystems often fail to return to the pre-disturbance condition. One of the most important concepts related to ecological resilience is the idea that complex systems can exhibit non-equilibrium conditions and exist in various alternative states that differ in processes, structures, functions, and feedbacks (Lewontin, 1969; Holling, 1973). The existence of non-equilibrium dynamics and alternative states has been demonstrated for numerous systems. The causes of shifts in states can arise from human perturbations such as nutrient enrichment, nitrogen deposition, acid rain from NOx and SOx, over-harvesting of fisheries and wildlife stocks, and inappropriate livestock grazing (Scheffer et al., 2001; Folke et al., 2004; Sasakia et al., 2015). They can also emerge over time

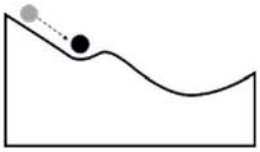
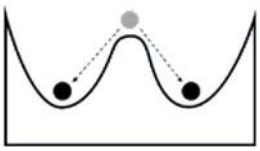
from a "command and control" approach in which management actions emphasize maximum output of one or few variables and ultimately reduce the range of natural variation in the system and result in a loss of system resilience, for example, by stabilizing river flows with dams, suppressing fires in fire-prone ecosystems, maximizing timber yield, or maintaining constant, high, deer populations (Holling and Meffe, 1996). Also, climate change may be further de-stabilizing processes, such as fire regimes (Westerling et al., 2006; Westerling, 2016; Littell et al., 2018) and affecting species distributions (Pecl et al., 2017; Shirk et al., 2018).

The actual shift in states may be triggered by stochastic events such as climatic extremes, disturbances like floods or wildfires, increased contagion of forest area, fuels, and forest density or insect outbreaks (Scheffer et al., 2001; Folke et al., 2004). They may also occur more gradually, for example, with changes in soil properties due to warming, nutrient enrichment, or acid rain that result in gradual species replacements, changes in functional group composition, and changes in trophic structures. Some of the best-studied examples include eutrophication of lakes and coastal oceans, shifts among grassy and woody cover types in rangelands, degradation of coral reefs, and regional climate change (Scheffer et al., 2001; Folke et al., 2004; Sasakia et al., 2015).

Systems can respond to disturbances or management actions in several different ways; developing an understanding of the tendency of a system to change states, and the factors influencing a change in state, is a key component of resilience-based management. The tendency of a system to shift states has often been illustrated using a ball and trough analogy. The size of the valley around a state (trough) is described as the basin of attraction and corresponds to the range of disturbance that a system (ball) can absorb without causing a shift to an alternative stable state, while the depth of the cup describes the intensity of disturbance that can be tolerated (Holling, 1973). Transitions among states are a function of the abiotic or biotic variables or events, acting independently or in combination, that contribute directly to loss of state resilience and result in shifts between states (Caudle et al., 2013). Thresholds represent the point at which there is an abrupt change in states, or where small changes in one or more external conditions produce large and persistent responses in an ecosystem (Angeler and Allen, 2016).

Some of the factors influencing a change in state for systems with high vs. low resilience are in **Table 2**. A system with a strong basin of attraction can absorb change and remain within the same state over a range of disturbances and management actions. These types of systems have been described as having relatively high ecological resilience (Scheffer et al., 2012). Conditions that contribute to a strong basin of attraction include favorable environmental conditions, strong feedbacks at multiple scales, and high levels of functional diversity and redundancy, which can stabilize the system and disturbances within the range of historic variability. A system with a weak basin of attraction may respond strongly to disturbance and move to an alternative state (**Table 2**). These types of systems have been described as having relatively low ecological resilience (Scheffer et al., 2012). Conditions that contribute to a weak basin of attraction include less favorable environmental conditions, inadequate species or functional groups to stabilize the systems, and disturbances that are outside of the range of historic variability. These systems typically represent the greatest challenge for managers as active management is often required and return to the initial state may not be possible if new conditions (e.g., increased CO_2, climate warming, changes in soil chemistry or structure, invasive species) are driving the state change. A system with more than one basin of attraction may respond to disturbance by changing states and moving to a new basin of attraction, but reorganize and return to the original state once conditions improve (**Table 2**). These types of systems have high adaptive

TABLE 2 | Ball and trough diagrams illustrating differences in the response of ecosystems to stressors and disturbances, the factors that contribute to ecological resilience and adaptive capacity, and the management implications [adapted from Scheffer et al. (2012)].

Resilience/Adaptive capacity	States and transitions	Contributing factors	Management options
High resilience		• Environment favorable • Species/functional groups stabilize system • Disturbances within HRV	• Strengthen capacity to adapt to environmental change • Prevent or minimize disturbances outside or the HRV
Low resilience		• Environment less favorable • Species/functional groups to stabilize system lacking • Disturbances outside ofHRV	• Prepare for anticipated change • Reduce risk of undesirable transition • Use opportunities to promote desired transitions
High adaptive capacity		• Changes in environment or magnitude of disturbance • Species/functional groups allow return to desired state • Disturbances within adaptive capacity	• Manage system for gradual adaptive response • Further strengthen the desired state

capacity to changes in environmental conditions (e.g., drought, flooding) or management (e.g., grazing, harvest rates).

Simple ball and trough diagrams help to conceptualize the changes possible in systems and the driving forces behind the changes, but in reality systems are highly complex and can exhibit multiple different trajectories and alternative states over time depending on the environmental factors, species and functional groups, and the type and characteristics of the disturbance. Also, system trajectories may be non-stationary due to a variety of internal and external drivers (Sundstrom et al., 2017). For example, with continued warming the relationship between climate and ecosystem responses to disturbances and management actions is likely to shift and managing for historical conditions may not maintain ecosystem goods, services, values, and biological diversity into the future (Millar et al., 2007; Hobbs et al., 2009). Recent analyses suggest that rather strong self-organization (positive feedbacks) keeps systems together, and that they may move in response to changing conditions unless or until a hard (e.g., mountain range) or incompatible boundary (strong soil difference) is reached (Allen et al., 2018; Roberts et al., 2018).

State-and-transition models (STMs) have long been used to describe the alternative states within ecosystems, factors causing the transitions, rates of transition, and potential restoration pathways. Range scientists and managers were among the first to adopt these concepts to describe changes in vegetation community composition due to factors such as drought, livestock grazing, and management actions (Archer, 1989; Westoby et al., 1989; Friedel, 1991; Laycock, 1991). Well codified STMs applicable to rangelands across the western U.S. have been developed by the USDA National Resources Conservation Service and their partners (Stringham et al., 2003; Briske et al., 2005; Bestelmeyer et al., 2009; Caudle et al., 2013). Most STMs developed for rangelands represent conceptual models based on expert opinion. However, empirically derived STMs have been used to relate plant community composition to factors such as climate, hydrologic regimes, soil processes, and management actions (Zweig and Kitchens, 2009; Karchergis et al., 2011; Bino et al., 2015), and to land-use change and changing disturbance regimes (Provencher et al., 2007; Daniel et al., 2016). Also, longer-term vegetation data have been used to evaluate transitions among communities, transition frequency, magnitude of accompanying compositional change, presence of unidirectional trajectories, and lack of reversibility within various timescales (Bagchi et al., 2012; Jamiyansharav et al., 2018).

Caution is needed when applying STMs to management problems. Most STM models require initial parameterization that involves assumptions about the numbers and types of states, their transition times, biotic and abiotic disturbances and stresses that create transitions or advance succession, and the frequency, patch sizes, and intensities of disturbances that might be expected. In essence, STMs do what the user tells them to do and consequently there is little opportunity for surprise. Thus, it is important to have relevant, independent datasets from the systems under observation, in order to validate and calibrate STM models before the results are accepted as representative of the modeled system (Keane, 2012).

Ecological, General, and Spatial Resilience

Integration of resilience concepts with landscape concepts provides the basis for understanding how ecosystem attributes and processes interact with landscape structure to influence the responses of ecosystems to disturbances and stressors and their capacity to support resources, habitats, and species over time. In this context, the concepts of ecological, general, and spatial resilience are interrelated (**Figure 1**, **Table 3**). The ecological resilience of ecosystems and general resilience of large landscapes is a function of environmental characteristics, disturbance regimes, ecosystem attributes and processes, and ecological memory (e.g., Chambers et al., 2014a, 2016b; Germino et al., 2016). Environmental factors, including climate, topography, and soils, determine the abiotic and biotic attributes of ecosystems. The disturbances with which ecosystems evolved, such as drought, extreme wet periods, fire, wind throw, and flooding, influence both abiotic and biotic ecosystem attributes and processes (Pickett and White, 1985; Pickett et al., 1989) and thus ecological memory (Peterson et al., 1998; Johnstone et al., 2016). Anthropogenic disturbances, management actions, and climate change act not only on the abiotic and biotic attributes and processes of ecosystems, but also on ecosystem disturbance regimes to affect ecological and general resilience over time.

In a landscape context, spatial resilience to disturbance is largely determined by the composition, configuration, and functions of patches within landscapes (**Figure 1**, **Table 3**). Spatial resilience is an emergent property of the spatial arrangement, differences, and interactions among internal elements (i.e., those within the focal system), external elements (i.e., those outside the focal system), and other spatially relevant aspects of resilience (Cumming, 2011a,b). Ecosystem disturbances and stressors influence spatial patterns and constrain processes, and processes, in turn, feedback to drive the dynamics of pattern in landscapes. Anthropogenic disturbances, management actions, and climate change affect patterns and processes and thus spatial resilience over time.

Understanding the multi-scale patterns and process within landscapes that determine ecological and spatial resilience provides the underpinning for resilience-based management. Landscapes are hierarchical in nature and the levels are cross-connected (panarchy; Angeler and Allen, 2016). Differences in interactions among climate, vegetation, and disturbance exist at patch, meso, and broad landscape scales, influence different aspects of ecological and spatial resilience, and inform different aspects of the planning process. Assessments of ecological and spatial resilience conducted at meso to broad scales can be used to inform budget prioritization for management actions, such as pre-positioning of firefighting resources and post-fire rehabilitation, across ecoregions or even biomes (Chambers et al., 2017a,c). An understanding of the factors that influence ecological and spatial resilience at patch to meso scales, coupled with local data and expertise, can be used to select project areas and determine appropriate

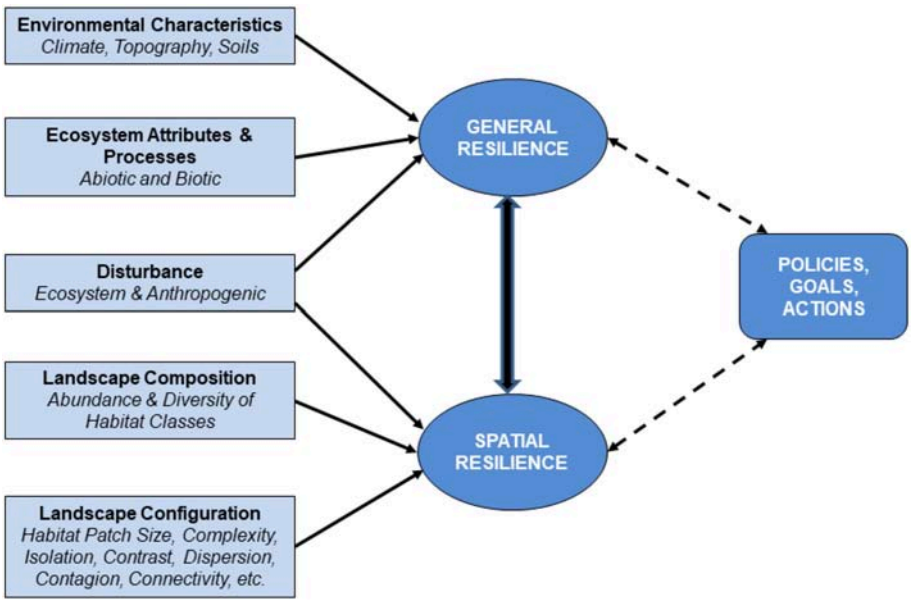


FIGURE 1 | Illustration of the primary factors that influence ecological, general, and spatial resilience. Ecological resilience of ecosystems and general resilience of large landscapes to ecosystem and anthropogenic disturbances is a function of environmental characteristics, ecosystem attributes and processes, and ecosystem and anthropogenic disturbances. In the context of landscapes, spatial resilience to disturbance is determined largely by the composition, configuration, and functions of patches within landscapes. An understanding of ecological, general, and spatial resilience provides the ability to develop resilience-based frameworks and decision support tools to inform management policies, goals, and actions.

TABLE 3 | Common disturbances and stressors, the factors that contribute to ecological, general, and spatial resilience to disturbances and stressors, and select indicator variables for each factor.

Disturbances and stressors	General resilience		Spatial resilience
	Environmental characteristics	**Ecosystem attributes and processes**	**Landscape context**
Ecosystem	*Climate*	*Abiotic*	*Landscape Composition*
- Drought/wet periods	- Precipitation	- Temperature and precipitation regimes	- Richness
- Fire	- Temperature	- Hydrologic fluxes and water storage	- Evenness
- Plant invasions	- Seasonality	- Geomorphic processes	- Diversity
Anthropogenic	*Topography*	*Biotic*	*Landscape Configuration*
- Agricultural, urban, and energy development	- Elevation	- Biological productivity	- Patch size distribution and complexity
- Over harvesting	- Slope and aspect	- Structure and composition	- Patch shape complexity
- Improper grazing	- Landform	- Functional groups, interactions, phenology, and traits	- Core area
- Species introductions	*Soils*	- Population regulation and regeneration	- Isolation/proximity
- Nutrient enrichment, N deposition, acid rain	- Depth and texture		- Contrast
- Rising CO_2, climate change	- %OM and nutrients		- Contagion and interspersion
- Restoration and mitigation efforts	- pH		- Subdivision
			- Connectivity

management strategies and treatments within areas prioritized for management (Chambers et al., 2017a,c).

Understanding ecological, general, and spatial resilience provides the capacity to develop resilience-based frameworks and decision support tools to inform management policies, goals, and actions (**Figure 1**). Geospatial information and knowledge of how the general resilience of ecosystems differs across large landscapes provides the basis for assessing relative ecosystem recovery potentials and risks of crossing critical thresholds (Chambers et al., 2017a,c; Ricca et al., 2018). Geospatial information and knowledge of how spatial resilience differs across the same landscapes provides the basis for evaluating spatial constraints on ecosystem recovery potential, availability of resources and habitats to support biodiversity, and connectivity among resources and habitats (Holl and Aide, 2011; Rudnick et al., 2012; McIntyre et al., 2014; Rappaport et al., 2015; Thatte et al., 2018; Kaszta et al., 2019). Combining information on ecological and spatial resilience with an understanding of the predominant ecosystem and anthropogenic disturbances and capacity to support habitats and species provides the basis for prioritizing management actions and determining effect strategies.

THE COMPONENTS OF RESILIENCE-BASED MANAGEMENT

A resilience-based approach for developing conservation and restoration priorities and determining effective strategies has several components (**Table 4**). Each of these components should be considered when developing resilience-based management plans for large landscapes.

Managing for Adaptive Capacity

Resilience-based management will be most effective when developed in the context of long-term adaptive management programs. Adaptive management reduces uncertainty in the effectiveness of, and responses to, management actions by evaluating and adjusting management objectives and strategies to improve the effectiveness of management actions over time. Integrated adaptive management programs are a form of structured decision making (*sensu* Gregory et al., 2012) that facilitate "learning by doing" and aid land managers and stakeholders in examining the context, options, and probable outcomes of decisions through an explicit and repeatable process (Allen et al., 2011; Williams, 2011; Marcot et al., 2012). A framework that includes evaluating the effects of environmental drivers and management interventions on ecological resilience can provide the basis for developing an increased understanding of resilience over time and incorporating that learning into management (Johnson et al., 2013; Brown and Williams, 2015). The first step of the process, assessment, involves defining the problem, identifying objectives, and determining evaluation criteria. Key components are assessing the available information and data and eliciting both input from experts (Runge et al., 2011) and feedback from stakeholders and partners (Gregory et al., 2012). Benchmarks and references for evaluating success are developed that account for the historic range of variability (Keane et al., 2009; Hessburg et al., 2013; Seidl et al., 2016) and ecological memory (Peterson et al., 1998; Johnstone et al., 2016), but factor in ongoing changes (Millar, 2014). In the next step, design, the alternatives are defined, consequences and key uncertainties identified, and tradeoffs evaluated. The preferred alternative is then determined, and the decision is made to implement the preferred alternative and management action(s). Long-term monitoring is the last step and is key to assessing

TABLE 4 | Key components of a framework for resilience-based management that informs conservation and restoration priorities and strategies.

Managing for adaptive capacity
- Adaptive management reduces uncertainty by enabling managers to evaluate and adjust objectives and strategies to improve effectiveness over time.
- Stakeholder and partner involvement increases effectiveness of decisions.
- Implementing management actions as experiments provides information on strategies that can increase adaptive capacity.
- Long term monitoring provides the information to adjust management as needed.

Selecting an appropriate spatial extent and grain
- Spatial extent and grain depend on the objectives and focal ecosystems or species.
- The spatial extent encompasses the characteristic range of variability within the landscape.
- Larger-scale conservation and restoration planning efforts include a wide variety of species to represent the diversity of species traits and habitat requirements within focal ecosystems.
- Organism-centric, multi-scale approaches are used for Threatened and Endangered species species in which landscapes are represented as gradients that influence organism occurrence, behavior, or performance.

Understanding key factors influencing the general and ecological resilience of ecosystems and landscapes
- Environmental factors differentiate ecosystems and indicate likely responses to disturbances and management actions.
- Ecosystem attributes and processes depend on environmental factors and further indicate responses to disturbances and management actions.
- Recurring ecosystem disturbances determine ecological memory and influence attributes and processes.

Understanding the importance of the landscape context
- The number, size, and spatial configuration of habitat fragments have substantial effects on restoration of ecosystems and conservation of focal habitats and species.
- Landscape connectivity facilitates movement among habitat patches, supports fluxes of energy, organisms, and materials, and maintains long-term persistence of ecosystems and biological diversity.
- Thresholds of landscape connectivity exist for focal ecosystems and organisms beyond which shifts in states occur and capacity to regain structure and function and provide habitats is lost.

Understanding key pattern and process interactions and their variability
- Changes in patterns, processes, and recovery rates are evaluated to gain insights into ecological and spatial resilience; characteristic ecosystem processes and higher recovery rates of those processes typically serve as indicators of higher adaptive capacity and resilience.
- Measurable, well-defined indicators and methods are required to evaluate disturbance effects.
- The historic range of variability in landscape patterns and processes can provide a baseline for evaluating changes in disturbance regimes and their effects on ecosystems and species.
- Landscape modeling can illustrate and clarify geospatial patterns of change resulting from disturbance, management actions, and climate change and identify thresholds of population decline.

Understanding relationships among ecological and spatial resilience and capacity to support habitats and species
- Species spatial distributions and relative abundances are closely related to a system's ecological and spatial resilience.
- Inclusion of a wide-variety of species to represent the diversity of species traits and habitat requirements within the system vs. use of indicator species requires careful consideration.
- Spatially explicit information on ecological and spatial resilience, disturbances, and locations and abundances of focal resources and species is used to ensure that areas selected for management actions support species populations and are beneficial.
- Spatially explicit, landscape genetic modeling of population connectivity, density, and effective population size provide powerful tools to investigate scenarios of altered disturbance regimes and management on biological processes and species populations.

effects of management actions on resilience and learning over time (Angeler and Allen, 2016). Monitoring is used to evaluate ecological status and trends and whether or not management objectives for increasing ecological resilience are met, and then to adjust management objectives and actions as needed.

Dealing with uncertainty is one of the greatest challenges in decision making. Changes in administrative priorities, policies, and economic resources can all cause uncertainty in the types of decisions that should be made as well as the outcomes of those decisions. Several well-recognized sources of uncertainty exist that are specific to making natural resource decisions (USDI, 2009; Conroy et al., 2011; Williams, 2011). ***First***, environmental uncertainty, or uncertainty in ecosystem and species responses to factors such as disturbances, weather events, climate change, and management actions, is a well-known source of uncertainty that characterizes all natural systems and requires little explanation. ***Second***, partial observability, or the need to estimate and model the relevant "quantities" that characterize natural systems because of our inability to directly observe nature, often limits our ability to accurately determine the resource "quantities" that are the targets of management. For example, the hectares of habitat to support a particular species are often estimated from limited research on habitat requirements, often in a different location. ***Third***, partial controllability, is the frequent inability to apply management actions directly and with high precision. This can lead to misinterpretation of the effectiveness of management actions. ***Fourth***, structural uncertainty, is the uncertainty in the models that predict system responses to specific management actions. Structural uncertainty is often represented by alternative models of system dynamics, each with associated measures of relative credibility. Reducing this type of uncertainty is a key objective of adaptive management (Runge et al., 2011).

Dealing with uncertainty in decision making requires recognizing its existence, establishing rules whereby an optimal decision can be made in the face of uncertainty, and reducing uncertainty where possible (Conroy et al., 2011; Williams, 2011). There is increasing recognition that effectively addressing uncertainty and facilitating decision-making in the context of adaptive management may require new laws, policies, guidelines, or funding structures (Garmestani and Benson, 2013).

Selecting an Appropriate Spatial Extent and Grain

For planning purposes, the landscape must reflect a meaningful spatial extent and grain for the focal ecosystems and species (Cushman et al., 2013), and be representative of the characteristic range of variability within the landscape (Keane et al., 2009; Wiens et al., 2012). Assessing a larger range of conditions than occurs within the focal landscape provides the necessary information on the typical or characteristic variability of a landscape with high ecological and spatial resilience relative to the landscape of interest (Keane et al., 2009; Keane, 2012). For example, to understand how a particular forest or shrubland type interacts with its fire regime and develop meaningful benchmarks for fuels treatments and other management actions, it is necessary to understand the range of characteristics and spatial extents of the areas that burned historically within the type.

In larger-scale conservation and restoration planning efforts, the spatial extent of the landscape should include a wide variety of species to represent the diversity of species traits and habitat requirements within the focal ecosystems (e.g., Fajardo et al., 2014). Resilience is posited to derive, in part, from the distribution of species diversity within and across scales (and in particular, the diversity of functional traits; Peterson et al., 1998). Ecological systems can often compensate for the loss or population reduction of single species, though resilience may be diminished (Sundstrom and Allen, 2014; Sundstrom et al., 2018).

For planning efforts involving threatened or endangered (T&E) species, an organism-centric, multi-scale approach has been advocated (e.g., McGarigal and Cushman, 2005; Cushman et al., 2010) in which landscapes are represented as a series of gradients that influence organism occurrence, behavior, or performance. These landscapes often occupy spatial scales intermediate between an organism's normal home range and its regional distribution, but may encompass the entire range of a species or subspecies confined to a particular biome or set of ecoregions. Thus, it is most pragmatic to consider landscapes as having a large extent (>1,000's−10,000's of hectares) composed of an interacting mosaic of ecosystems and encompassing populations of many species.

In many cases, landscape boundaries are linked to management jurisdictions, such as parks or reserves (e.g., Schweiger et al., 2016). Landscapes defined by humans may or may not correspond with natural boundaries or spatial regimes (Sundstrom et al., 2017; Roberts et al., 2018). Identifying scales in ecosystems has been a major effort of resilience research in recent years; techniques have been described in Angeler and Allen (2016) and Allen et al. (2016), and include discontinuity analysis (Allen and Holling, 2008), Fisher Information (Spanbauer et al., 2014) and Multivariate Time Series Modeling (Angeler et al., 2016). The idea of spatial regimes has been used to identify self-similar, self-organizing, but non-stationary geographic regions. Combining spatial regime approaches with techniques that can identify natural scaling within a given regime holds promise for increasing understanding of spatial resilience in terrestrial ecosystems.

Understanding Key Factors Influencing the General and Ecological Resilience of Ecosystems and Landscapes

An understanding of the ecological and general resilience of ecosystems and landscapes provides the necessary information to (1) evaluate the differences in ecosystem responses to disturbance and their recovery potentials across landscapes, and (2) identify locations where ecosystems may exhibit critical transitions to novel alternative states in response to altered local or global drivers. Resilient ecosystems and landscapes have the ability to return to the prior or desired state.

Environmental characteristics are typically strong indicators of general and ecological resilience and are important factors in resilience-based assessments (**Figure 1**; **Table 3**). The early resilience literature identified the importance of a system's

underlying environmental characteristics in determining the response of its component ecosystems to disturbance (Pickett and White, 1985; Pickett et al., 1989) at biome to patch scales (MacMahon, 1981; Turner, 1989; Wu and Loucks, 1995). Temperature coupled with amount and seasonality of precipitation largely determines the dominant life forms, ecological types, and productivity of ecosystems. An ecosystem's general resilience typically decreases as climatic conditions become more extreme (e.g., cold temperatures, hot temperatures coupled with low precipitation, low and variable precipitation; MacMahon, 1981). For example, amount of precipitation has been shown to strongly influence general resilience to changes in annual precipitation and other drivers at continental and regional scales. On the continents of Africa, Australia, and South America, spatial analyses of tree cover and annual precipitation indicate that changes in the general resilience of tropical forest, savanna, and treeless states varies in a universal way with precipitation and show where forest or savanna may most easily shift into an alternative state (Hirota et al., 2011). Relationships among seasonality of precipitation and growing season temperature also affect general resilience at regional scales (e.g., Paruelo and Lauenroth, 1996; Sala et al., 1997; Levine et al., 2016).

Ecosystem attributes and processes are important factors in analyses of general resilience and can include land cover of vegetation types, productivity indices, species functional traits, and modeled ecosystem processes, such as soil temperature and moisture regimes (Bradford et al., in press), and ecophysiological processes (Levine et al., 2016; **Table 3**). Longer term data on effects of disturbances and management actions and climate change projections make it possible to assess ecosystem state changes over time and to evaluate the potential for climate-induced thresholds (Hirota et al., 2011; Levine et al., 2016). For example, in Amazonia, remote-sensing and ground-based observations combined with size- and age-structured terrestrial ecosystem models demonstrate that water stress operating at the scale of individual plants, along with the spatial variation in soil texture, explains observed patterns of variation in ecosystem biomass, composition, and dynamics across the region, and strongly influences the response of the different ecosystems to changes in dry season length (Levine et al., 2016).

In a wide variety of systems, general and ecological resilience vary over environmental gradients at small landscape scales where aspect, slope, and topographic position affect solar radiation, erosion processes, effective precipitation, and soil development and, thus, the composition, structure, and productivity of communities. These environmental gradients influence land uses, such as livestock grazing (Bestelmeyer et al., 2011), disturbance patterns, such as the occurrence and severity of wildfires (Hessburg et al., 2016), ecosystem responses to those land uses and disturbances (e.g., Condon et al., 2011; Davies et al., 2012; Spasojevic et al., 2016), and restoration potential (Holl and Aide, 2011; de Souza Leite et al., 2013).

Integrated analyses of longer-term geospatial data, field data, and historical reconstructions provide the basis for understanding effects of disturbances on ecosystem attributes and processes over time and thus their ecological memory (Johnstone et al., 2016). The ecological memory of ecosystems is strongly associated with ecological and general resilience (Peterson et al., 1998; Peterson, 2002). Recurring ecosystem disturbances with characteristic frequency, severity, size, or other attributes influence geomorphic and hydrologic process and affect biogeochemical processes. These disturbances also exert strong selective pressure on species life-history strategies, which affect population survival and spread (Keeley et al., 2011). The processes, traits, individuals, and materials that persist after a disturbance, or the ecological memory of the system, shape responses to future disturbance (Johnstone et al., 2016). Ecological memory may be encoded across a range of spatial and temporal scales, from small, patch-scales to broad landscapes, and from decadal to evolutionary timescales (Johnstone et al., 2016).

In the context of landscapes, both the environmental characteristics and ecological memories of the focal systems influence general resilience. For example, in the four-corner region of the USA, remote sensing and species trait databases were used in combination with path analyses to evaluate if functional diversity across a range of woodland and forest ecosystems influences the recovery of productivity after wildfires (Spasojevic et al., 2016). Both topography (slope, elevation, and aspect) and functional diversity in regeneration traits (fire tolerance, fire resistance, ability to resprout) directly or indirectly influenced the recovery of productivity after wildfires.

Understanding the Importance of the Landscape Context and Spatial Resilience

An understanding of spatial resilience in the context of landscapes provides the necessary information for creating structurally and functionally connected networks that provide ecosystem services and conserve resources and species. Landscape patterns can either facilitate or impede the flow or movement of individuals, genes, and ecological processes. The landscape context is a critical element in both restoration and conservation ecology for (1) understanding the effects of disturbance on landscape patterns and processes, (2) evaluating the number, size, and spatial configuration of habitat fragments and degree of connectivity required to support restoration of ecosystems and conservation of focal habitats and species, and (3) determining thresholds of connectivity beyond which the capacity to regain structure and function is lost (Holl and Aide, 2011; Rudnick et al., 2012; McIntyre et al., 2014; Rappaport et al., 2015; Ricca et al., 2018).

Measuring metrics of the composition and configuration of landscapes (e.g., McGarigal et al., 2012) (**Table 3**) provides a quantitative framework to assess spatial structure and relate it to spatial resilience. Quantifying the range of states within a system in the context of landscape patterns under different disturbance and other process regimes is a core element of quantifying spatial resilience. A wide variety of tools and models exist for identifying landscape pattern metrics that provide interpretable (Neel et al., 2004) as well as consistent, universal, and strong

measures of major attributes of landscape spatial structure (Cushman et al., 2008).

The landscape context can be as important as its general resilience and local site characteristics in influencing restoration effectiveness via effects related to the amount of habitat cover, connectivity among habitats, and relative isolation (de Souza Leite et al., 2013; Tambosi et al., 2014). Restoration effectiveness generally increases for restored areas in close proximity to neighboring patches and in landscapes with high habitat cover (see review in de Souza Leite et al., 2013). It also decreases with progressive changes in landscape development over time (Rappaport et al., 2015). Effects of landscape characteristics on restoration outcomes may vary with species characteristics and differ according to the population or community parameters (e.g., abundance, richness, composition) considered (de Souza Leite et al., 2013). Also, different landscape aspects mediate the effects of restoration actions on ecosystems, and the landscape metrics used for planning and monitoring need to be tailored to the system of interest.

The landscape context and spatial resilience are a central part of modern conservation ecology. The spatial composition and configuration of habitat plays a critical role in affecting species persistence (With and King, 1999); long-term persistence requires a sufficient number, size, and spatial configuration of habitat fragments (Hanski and Ovaskainen, 2002). The habitat requirements of species are individualistic, because each species has a unique ecological niche, which differs from that of all other species; multidimensional, because several to many important environmental variables typically define each species' habitat; and multiscale, because each of these environmental variables is likely to be related to space or other resource use at different spatial scales (e.g., Grand et al., 2004; Wasserman et al., 2012). For example, bald eagle habitat selection is driven by a number of environmental variables, but selection of each kind of habitat (such as for foraging or roosting locations) is driven by different variables at different scales (Thompson and McGarigal, 2002).

The "metapopulation capacity" is the likelihood of long-term population viability given a particular extent, configuration, and quality of habitat. Habitat loss and fragmentation reduce the metapopulation capacity of a landscape and make extinction more likely. Thus, in addition to knowing the extent and quality of the remaining habitat, identifying the habitat's spatial configuration and connectivity is essential to determining the effects on population size (Ovaskainen, 2002). The adverse effects of habitat loss and fragmentation on biodiversity can be divided into two dominant categories. First, as habitat is lost from the landscape, at some point there will be insufficient area of habitat to support a population, and the species will be extirpated from the landscape (Flather and Bevers, 2002). This is referred to as the *area effect*. Second, as habitat is lost and fragmented, individual habitat patches become more isolated from one another. As populations become subdivided, the movement of individuals among habitat patches (e.g., dispersal) may decrease or cease altogether, which may affect critical metapopulation processes such as gene flow, demographic rescue, and recolonization following local extinction (Fahrig and Merriam, 1994). This is referred to as the *isolation effect*.

Landscape connectivity is the ability of a landscape to facilitate or impede movement among habitat patches, support fluxes of energy, organisms and materials (e.g., seeds, biomass, pollen, nutrients, sediments) and maintain long-term persistence of both ecosystems and biological diversity (Saura and Pascual-Hortal, 2007; Foltête et al., 2012; Ng et al., 2013). It is a function of both the characteristics of the landscape (structural connectivity) and organism mobility (functional connectivity). A well-connected landscape enhances the spatial resilience of systems, allowing them to overcome sudden changes (e.g., climate changes, wildfires) by persistence, adaptation, and transformation processes. A reduction in landscape connectivity can be considered an early-warning indicator of shifts among stable or metastable states of systems (Zurlini et al., 2014). Landscape connectivity has been used as a surrogate for spatial resilience in ecoregional planning for wildlife (Cushman and Landguth, 2012; Cushman et al., 2016, 2018), forest (Theobald et al., 2011) and invasive species management (Alistair et al., 2013). It has also been used to evaluate the loss of individual wetlands in wetland complexes (Uden et al., 2014) and ecosystem provisioning for humans (Wu, 2013).

Landscape connectivity is an important measure of the spatial resilience of systems to climate change and other perturbations. For example, climate controls connectivity among prairie wetlands for migratory birds within and across the three main wetland complexes in the Great Plains of North America (McIntyre et al., 2014). Climate projections and bird species data suggest that changes in precipitation patterns due to climate change will likely reduce wetland network density and connectivity and result in reduced bird abundance where dispersal capacity will be as important as wet/dry conditions (McIntyre et al., 2014).

Thresholds of connectivity can be identified beyond which systems shift states and lose the capacity to provide resources and habitats (Frair et al., 2008; Thatte et al., 2018; Kaszta et al., 2019). For example, dense human settlements and roads with high traffic are detrimental to tigers (*Panthera tigris*) in Central India. Landscape genetics analyses and spatially-explicit simulations were used to examine current population connectivity of tigers across nine reserves (Thatte et al., 2018). Landscape genetic simulations modeled potential impacts of different scenarios of future land-use change and found that genetic variability (heterozygosity) will likely decrease in the future and small or isolated populations will have a high risk of local extinction. Scenarios where habitat connectivity was enhanced and maintained, stepping-stone populations were introduced/maintained, and tiger numbers were increased, led to lower overall extinction probabilities. As another example, to evaluate effects of alternative development and conservation scenarios on clouded leopards (*Neofelis nebulosa*) across Sabah, Borneo, coupled individual-based population, and genetic models were used (Kaszta et al., 2019). Landscape connectivity was highly correlated with predicted local population density and genetic diversity of clouded leopards, and there were substantial differences in how much each scenario impacted the distribution, abundance, and genetic diversity of the species.

Understanding Key Pattern and Process Interactions and Their Variability

Information on extents and patterns of disturbances and their interactions with ecosystem attributes and processes facilitates land use planning and enables selection of effective management strategies. Assessments can be designed to (1) evaluate the extents and magnitude of ecosystem and anthropogenic disturbances, (2) assess status and trends based on a recent history, and (3) identify thresholds of change in structure and function.

The impacts of disturbances on landscape pattern, structure, and function drive most ecosystem processes and ultimately set the bounds of management for most landscapes of the world (Keane et al., 2009). Ecosystem disturbance regimes describe the temporal and spatial characteristics of a disturbance agent; specifically, the cumulative effects of multiple disturbance events over space and time. Descriptions of disturbance regimes must encompass an area that is large enough so that the full range of disturbance sizes are represented, and long enough so that the full range of disturbance characteristics are captured (Keane et al., 2009). Anthropogenic disturbances, climate change, and management actions interact with ecosystem disturbance regimes and are essential considerations when quantifying and describing disturbance effects on general, ecological, and spatial resilience.

Changes in patterns, processes, and recovery rates under altered disturbance regimes can be evaluated to gain insights into ecological and spatial resilience, with characteristic ecosystem processes and higher recovery rates of those processes typically serving as indicators of higher adaptive capacity and resilience (Chambers et al., 2014a; Seidl et al., 2016). Measurable, well-defined indicators and methodologies are required to evaluate the effects of changes in ecosystem disturbance regimes and the interacting effects of anthropogenic disturbance (Angeler and Allen, 2016). Quantifying changes in disturbance and effects on pattern and processes requires a temporal dimension that can be obtained through long-term monitoring and datasets. In most cases, process-based approaches will be most useful for monitoring and assessing changes in ecological and spatial resilience over time (e.g., Lam et al., 2017).

The historical range of variation (HRV) has been used to assess ecological status and change by assuming recent historical variation represents the broad envelope of conditions (basin of attraction) that supports the self-organizing capacity of landscapes and thus resilience (Hessburg et al., 1999; Keane et al., 2009; Seidl et al., 2016). The historical range of variation (HRV) is based on the idea that the broad historical envelope of possible ecosystem conditions, such as disturbed area, vegetation cover type area, or patch size distribution, can provide a representative time series of reference conditions to guide land management (reviewed in Keane et al., 2009). The HRV is typically based on longer-term geospatial data from remote sensing, field data, and historical reconstructions. The available empirical data can be used to parameterize landscape simulation models, which then simulate ecological processes and extrapolate parameter values across entire regions (Keane, 2012).

The HRV has been used by managers to define ecological benchmarks for determining status, trend, and magnitude of change, and develop objectives and strategies for conservation and restoration management. Application of HRV concepts include prioritizing and selecting areas for possible restoration treatments (Reynolds and Hessburg, 2005; Hessburg et al., 2007, 2013) and identifying areas for conservation of biological diversity (Aplet and Keeton, 1999). Applying the HRV concept has been challenging because the scales of climate, vegetation, and disturbance interactions are inherently different across landscapes, field data in adequate abundance and appropriately scaled are seldom available to define HRV characteristics at many scales, and few statistical techniques exist to compare HRV time series data to current landscape composition and structure (Keane et al., 2009). Recent criticisms of HRV concepts are that historical conditions do not serve as a proxy for ecological resilience in this era of global change (Millar, 2014) and large-scale inferences for entire regions or ecosystems, such as for historical fire regimes, often entail substantial uncertainty and can yield equivocal results (Freeman et al., 2017).

Recently, spatially explicit models have been used to inform management planning processes and help define ecological benchmarks for determining status, trend, and magnitude of change, typically in a risk assessment framework. The interacting effects of ecosystem and anthropogenic disturbances on landscapes and species have been modeled for a wide-variety of landscapes and disturbance types to inform land use plans (e.g., Cushman et al., 2017; McGarigal et al., 2018; Ricca et al., 2018). Longer-term trends in climate have been used to forecast future variations of landscape patterns and processes using highly complex spatial empirical and mechanistic models to increase understanding of disturbance interactions (Loehman et al., 2017) and inform selection of indicators of ecological and spatial resilience (Bradford et al., in press). Like HRV simulation models, these models also entail uncertainties that must be recognized when developing management objectives and monitoring protocols and adapting management to changing conditions.

A primary role of landscape modeling is to clarify and illustrate patterns of risk over time. For example, Cushman et al. (2017) modeled the spatial pattern of risk of forest loss between 2010 and 2020 across Borneo as a function of topographical variables and landscape structure. They found that a random forest modeling framework, which uses landscape metrics as predictors at multiple scales, can be a powerful approach to landscape change modeling. Risk of forest loss differed among Borneo's three nations as a function of distance from the edge of the previous frontier of forest loss and the structure of the landscape, but in general very high rates of forest loss were predicted across the full extent of Borneo. Maps produced for the project showed clear spatial patterns of risk related to topography and landscape structure.

Landscape modeling and geospatial data can be used to evaluate the effects of landscape fragmentation and identify thresholds of change beyond which species population abundance declines. Resilience-based land use plans can be informed by data on hypothesized or observed thresholds,

including in disturbance characteristics, population abundance, and landscape connectivity, and the likely impact of crossing those thresholds. Information on time lags and regional variation further informs these plans. For example, rapid expansion of energy development in some portions of the Intermountain West, USA, has prompted concern regarding impacts to declining Greater sage-grouse (*Centrocercus urophasianus*) populations. Potential thresholds in the relationships among lek attendance by male greater sage-grouse, the presence of oil or gas wells near leks (surface occupancy), and landscape-level density of well pads were developed using generalized linear models and generalized estimating equations (Harju et al., 2010). Surface occupancy of oil or gas wells adjacent to leks was negatively associated with male lek attendance, but time-lag effects suggested that there is a delay of 2–10 years between activity associated with energy development and its measurable effects on lek attendance.

Understanding Relationships Among General, Ecological, and Spatial Resilience and Capacity to Support Habitats and Species

Species spatial distributions and relative abundances are closely related to general, ecological, and spatial resilience. General and ecological resilience are related to climatic factors that determine species distributions, i.e., the bioclimatic range, and ecosystem attributes and processes that determine habitat suitability, such as availability of food, nutrients, and water. Spatial resilience is related to pattern and process interactions that affect gene flow, dispersal, and migration. Disturbance influences resilience through effects on the bioclimatic envelop and resource availability, such as extreme events like droughts or heat-waves and spatial resilience through factors that affect local movements, dispersal, and migration, such as development and transportation and energy corridors. Threshold crossings of both ecological and spatial resilience are indicated by decreases in species occurrence, abundance, and use or non-use of habitat.

The spatial scales and types of data used to evaluate the interrelationships of general and spatial resilience with capacity to support biological diversity depend on the management objectives and the focal landscape. Larger-scale conservation planning efforts ideally include a wide-variety of species to represent the diversity of species traits and habitat requirements within the focal landscape (e.g., Fajardo et al., 2014). In practice, indicator species or other surrogates are often used to monitor environmental changes, assess the efficacy of management, and provide warning signals for impending ecological shifts (see reviews in Jørgensen et al., 2013; Siddig et al., 2016). This approach is not without criticism and there should be strong justification for the species selected as indicators (Dale and Beyeler, 2001; Carignan and Villard, 2002; Cushman et al., 2010; Siddig et al., 2016). Considering the causes and effects of changes in populations beyond the predominant disturbances may improve change detection and thus management recommendations (Carignan and Villard, 2002). Including different taxa with varying affinities to the ecosystems within the system, spatial requirements, and sensitivities to the predominant disturbances may help identify the causes of change more precisely and limit errors of interpretation. The increasing availability of data, statistical tools, and comprehensive models relating species to resilience supports multi-species approaches (Sundstrom et al., 2018).

Ecological and spatial resilience have direct application to conservation management of threatened and endangered species. Spatially explicit information on a system's ecological and spatial resilience, predominant disturbances, and locations and abundances of focal resources and species provides information for evaluating the likely success of different types of management strategies. An understanding of the ecological resilience of the ecosystems that provide habitat for the focal species provides information on the management strategies most likely to succeed (e.g., Chambers et al., 2017a,c). Linking landscape metrics, such as patch size, shape, and connectivity, with landscape occupancy and use of focal species or species distribution models helps further ensure that areas selected for management support populations of the focal species, provide connectivity among populations, and are close enough to breeding centers for recolonization (Guisan and Thuiller, 2005; Doherty et al., 2016; Ricca et al., 2018). New approaches such as spatially explicit, individual-based population, and genetic models (e.g., Landguth and Cushman, 2010) and landscape genetic modeling of population connectivity, density and effective population size as functions of landscape structure (e.g., Balkenhol et al., 2016) provide powerful tools to directly investigate scenarios of altered disturbance regimes and landscape management on biological processes and species populations (e.g., Hearn et al., 2018; Macdonald et al., 2018; Thatte et al., 2018; Kaszta et al., 2019).

A RESILIENCE-BASED APPROACH FOR PRIORITIZING AREAS FOR MANAGEMENT AND SELECTING APPROPRIATE STRATEGIES

A strategic, multi-scale approach to management can be used to address the rapid changes occurring in global ecosystems. Knowledge of general and spatial resilience to disturbance coupled with information on key resources, habitats, or species and the predominant disturbances can be used to facilitate regional planning. Use of a spatially explicit approach can enable managers to quantify and visualize differences in resilience in relation to focal resources and disturbances, and then to both prioritize areas for management actions and determine the most effective strategies. Assessments conducted at meso to broad scales can be used to inform ecoregional to biome prioritization of management actions across large landscapes and to allocate budgets and manpower in a manner designed to maximize attainment of conservation and restoration objectives. Knowledge of ecological and spatial resilience at patch to meso scales based on literature review, and local data and expertise, can be used to select project areas and determine appropriate management strategies within areas prioritized for management (Chambers et al., 2017a,c; Crist et al., 2019). We

illustrate this type of multi-scale, resilience-based framework for addressing ecosystem and anthropogenic disturbances with a case study from a highly imperiled area of the western U.S. —the sagebrush biome.

Application of the Resilience-Based Framework in the Sagebrush Biome

The sagebrush biome spans ∼100 million hectares in western North America. Sagebrush ecosystems occur across broad environmental gradients and provide a large diversity of habitats that support more than 350 species of vertebrates (Suring et al., 2005). These ecosystems currently make up only about 59 percent of their historical area. The primary patterns, processes, and components of many sagebrush ecosystems have been significantly altered since Euro-American settlement in the mid-1800s (Knick et al., 2011; Miller et al., 2011). The predominant disturbances in sagebrush ecosystems are large-scale wildfire, invasion of exotic annual grasses, conifer expansion, energy development, conversion to cropland, and urban and exurban development (Davies et al., 2011; Knick et al., 2011; FWS, 2013; Coates et al., 2016). The continued loss and fragmentation of sagebrush habitats has placed many species at risk, including Greater sage-grouse (*Centrocercus urophasianus*; hereafter, GRSG), which was considered for listing under the U.S. Endangered Species Act in 2010 and 2015 (FWS, 2010; USDI FWS, 2015) and whose status will be reevaluated in 2020 (USDI FWS, 2015).

GRSG are a broadly distributed species that occupy a variety of environments containing sagebrush. They have been managed as umbrella species for the many other species of plants and animals that depend on sagebrush ecosystems (Suring et al., 2005; Knick et al., 2013). Listing of GRSG as an endangered species would place numerous restrictions on land uses (e.g., livestock grazing, energy exploration, and development) in those sagebrush ecosystems that provide habitat for the species and thus has widespread political and management ramifications. A high percentage of the land within the sagebrush biome is managed by state and federal agencies (ranging from 85% in the State of Nevada to 29% in the State of Montana) placing increased pressure on these agencies to develop effective conservation and restoration approaches.

A collaborative, interagency working group has developed a strategic, multi-scale framework based on resilience science to address the continued loss of sagebrush habitat and declines in GRSG populations (Chambers et al., 2014c, 2016a, 2017a,b; Crist et al., 2019). The resilience-based framework provides the geospatial data, analytical approaches, and decision support tools for prioritizing areas for management and determining effective strategies across the sagebrush biome (**Figure 2**). The framework is founded on understanding (1) general resilience, as indicated by environmental characteristics and ecosystem attributes and processes, (2) spatial resilience, based on landscape composition and configuration, and thus capacity to support high value resources, and (3) interactions of general and spatial resilience with the predominant disturbances. In-depth knowledge of the multi-scale patterns and process within sagebrush landscapes that determine resilience has been key to developing the framework (**Box 1**). Use of this multi-scale, resilience-based framework to address invasive grass-fire cycles in arid and semiarid shrublands and woodlands is illustrated in a companion paper in this journal (Chambers et al., 2019).

The multi-scale, resilience-based framework described herein has been used by the U.S. Forest Service to develop fire risk assessments for all Forest Service lands that support GRSG and for the Intermountain Region. The concepts and approaches in the framework were incorporated into the "Department of the Interior's Integrated Rangeland Fire Management Strategy" (USDI, 2015) and have been used by the Bureau of Land Management to develop a multiyear program of work for Bureau of Land Management managed lands in the western part of the sagebrush biome.

Key Components

1. Management Objectives

   Objectives for addressing loss of sagebrush habitat and declines in GRSG populations provide the basis for managing ecosystems to increase their capacity to reorganize and adjust to ongoing change while providing necessary ecosystem services. Overarching management objectives focus on both sagebrush ecosystems and GRSG populations and include:

- Increasing or maintaining resilience to disturbance and resistance to invasive annual grasses in sagebrush ecosystems across the biome.
- Ensuring the long-term conservation of GRSG by maintaining viable, well-distributed GRSG populations that are connected by healthy sagebrush ecosystems across their range.

A collaborative approach that includes federal and state agencies and other partners, such as non-governmental organizations, tribes, and private land owners, is used to develop management objectives for specific planning areas. Long-term monitoring is being implemented within the land management agencies to provide the capacity to adapt management over time and help ensure long-term success. For example, status and trend is monitored through the Bureau of Land Management's Assessment Inventory and Monitoring; Natural Resources Conservation Service's National Resources Inventory, both of which use common indicators and protocols.

2. Landscape Indicators of General Resilience and Resistance to Invasive Grasses

   In sagebrush ecosystems, soil temperature and moisture regimes closely reflect climate and vegetation patterns and provide one of the most complete data sets for understanding and visualizing general resilience to disturbance and resistance to invasive annual grasses across the sagebrush biome (see reviews in Brooks et al., 2016; Chambers et al., 2016b, 2019; also Ricca et al., 2018; Bradford et al., in press). They have been mapped for most of the sagebrush biome and are available through the USDA Natural Resources Conservation Service, Web Soil Survey (https://websoilsurvey.nrcs.usda.gov). The dominant vegetation (ecological) types differ across the sagebrush biome and have been characterized

according to soil temperature and moisture regimes, general resilience to disturbance, and resistance to invasive annual grasses (Chambers et al., 2017a) based on recent research (Chambers et al., 2007, 2014b, 2017b; Condon et al., 2011; Davies et al., 2012; Urza et al., 2017) and expert input. State-and-transition models, which provide information on the alternative states, ranges of variability within states, and processes that cause plant community shifts within states as well as transitions among states, have been developed for the dominant vegetation types (Chambers et al., 2017a). To facilitate landscape analyses and prioritization, soil temperature, and moisture regime subclasses have been used to categorize relative resilience to disturbance and resistance to invasive annual grasses as high, moderate, or low across the sagebrush biome (**Figure 3**; Maestas et al., 2016; Chambers et al., 2017a). Higher resolution categories can be developed for assessments conducted at ecoregional or sage-grouse Management Zone scales and detailed soils data are available for project area assessments.

3. Spatial Resilience and GRSG Populations

The breeding habitat model for GRSG (Doherty et al., 2016) provides one the best sources of information for understanding and visualizing spatial resilience in the context of GRSG populations. The breeding habitat model uses GRSG lek data (2010–2014) as a proxy for landscapes important to breeding birds. Leks are central to the breeding ecology of GRSG and the majority of nests occur relatively close to leks (within 6.3 km; Holloran and Anderson, 2005; Coates et al., 2013). The breeding habitat model evaluates the vegetation (i.e., landscape cover), climate, and landform characteristics as well as the type and amount disturbance around leks (within a radius of 6.4 km; Doherty et al., 2016), and provides

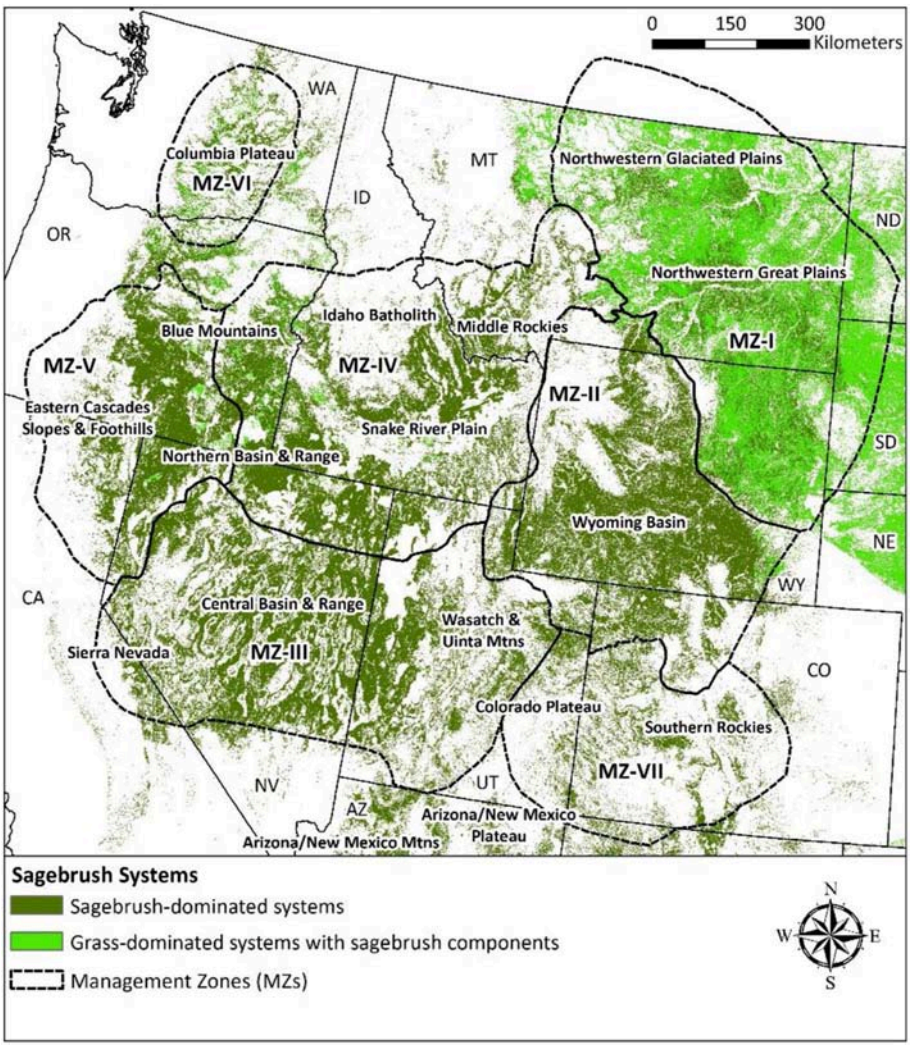


FIGURE 2 | A map of the landscape cover of sagebrush-dominated ecological systems and grass-dominated ecological systems with sagebrush components in the sagebrush biome (Chambers et al., 2017a). The landscape cover of sagebrush (USGS, 2016) is overlaid on Level III Ecoregions (USEPA, 2017) and sage-grouse Management Zones (Stiver et al., 2006).

Box 1 | The factors that influence the ecological (ER), general (GR), and spatial resilience (SR) of Cold Desert ecosystems and landscapes to wildfires and non-native grass invasions at patch and patch neighborhood, meso, and broad scales (based on Chambers et al., 2019). In these ecosystems ecological and general resilience to wildfires and resistance to non-native grass invasions varies over environmental gradients as a function of soil temperature and moisture regimes, productivity, historic fire regimes, and species adaptations to fire, as well as resistance to invasive annual grasses. Spatial resilience differs as a result of relative abundance of the dominant life forms (composition) and their spatial relationships (configuration). The patterns and processes that influence ecological and spatial resilience are linked, but are unique to each scale. The descriptions here represent endpoints of conditions across large landscapes.

Patch and patch neighborhood scale. Shrub size, composition, and abundance of perennial herbaceous species, and gap sizes among shrubs and herbaceous species influence resource availability, competitive interactions, and invasion of flammable invasive annual grasses, which in turn influence wildfire dynamics.

Low ER–Soils are warm and dry and productivity is relatively low. Low fuel biomass resulted in few historic fires, and plant species have few adaptations to fire. High climate suitability to invasive annual grasses (IAG) results in low resistance to their invasion. Recovery potentials depend on abundance of perennial native herbaceous species (PNH) that survive fires and resource availability for invaders.

➢ *SR*–In patches with high SR, PNH are relatively abundant. Small gap sizes among PNH result in strong competition and low abundance of IAG. Large gap sizes among shrubs decrease fire severity and abundant PNH result in site recovery after fire. Patches with low SR have the opposite conditions.

High ER–Soils are cool to cold and moist and productivity is high. High fuel biomass and historically short fire return intervals resulted in fire-adapted plant species. Low climate suitability to IAG results in high resistance to their invasion. Recovery potentials are typically high.

➢ *SR*–In patches with high SR, PNH are relatively abundant with small gap sizes among PNH. Large gap sizes among shrubs decrease fire severity and abundant, fire-tolerant shrubs, and PNH result in site recovery after fire. Low SR has the opposite conditions, but recovery potential is still moderately high.

Meso scale. Wildfire and invasion patterns, amount of fine fuel, fuel conditions, and fire weather influence fire event sizes and fire severity patch size distributions, which themselves create opportunities for restoration as well as invasion and affect future disturbances.

Low GR–Ecosystems are fuel-limited and had low fire return intervals historically. Invasion of IAG into shrublands increases fine fuels and flammability. Fine fuel availability and fire probability depends on antecedent precipitation. Improper livestock grazing increases woody fuels and fire severity. Large fire size is linked to extreme fire weather.

➢ SR–Areas with high SR have relatively high landscape cover of PNH, relatively high shrub cover, low cover of IAG, and low burned area. Areas with low SR have relatively low cover of PNH, high landscape cover of IAG, and high burned area.

High GR–Ecosystems are flammability or drought limited and had higher fire return intervals historically. Warmer and drier conditions decrease fuel moisture sufficiently for large wildfires to burn. Improper livestock grazing increases woody fuels and fire severity. Large fire size is linked to extreme fire weather.

➢ SR–Areas with high SR have relatively high landscape cover of PNH, relatively high shrub cover, a mosaic of small burned areas, and high connectivity. Areas with low SR have reduced cover of PNH and shrubs, extensive burned areas, and low connectivity. SR can be reduced by anthropogenic disturbances, such as oil and gas drilling, agriculture, and urban development, regardless of general resilience.

Broad ecoregional scale. Patterns of biophysical conditions influence broad scale invasion patterns and the fire delivery system, and determine fire size and severity and expansion of the invader.

GR–The climatic regime (relative aridity and seasonality of precipitation) influences the relative proportion of woody vs. perennial herbaceous species, fire seasonality and burned areas, and climactic suitability for IAG. Landscape heterogeneity and environmental conditions determine the proportions of ecosystems with low, moderate, and high ER. Landscapes with a higher proportion of low ER ecosystems, lower resistance to IAG, and higher fire risk have lower ER. High ER landscapes have the opposite conditions.

➢ SR–Landscapes with high SR are characterized by relatively low aridity and summer-dominated precipitation. Landscape cover of PNH and shrubs is relatively high, cover of IAG is low, and burned areas are within the historic range of variability. Landscapes with low SR are characterized by relatively high aridity and winter-dominated precipitation along with reduced landscape cover of PNH and shrubs, and higher landscape cover of IAG, and higher burned areas. SR can be reduced by anthropogenic disturbances, such as oil and gas drilling, agriculture, and urban development, regardless of general resilience.

an estimate of the probability of occurrence of breeding sage-grouse at a spatial resolution of 120 × 120 m. Model output is specific to the habitat characteristics of each sage-grouse Management Zone.

Breeding habitat probabilities for GRSG in Doherty et al. (2016) were used to develop three categories of breeding habitat probability for prioritizing management actions across large landscapes (**Figure 4**; Chambers et al., 2016a, 2017a). The categories were based on the probability of areas near leks (within a radius of 6.4 km) providing suitable breeding habitat and included: low (0.25 to <0.50); moderate (0.50 to <0.75); and high (0.75 to 1.00). Areas with probabilities of 0.01 to <0.25 were considered to be unsuitable for breeding habitat. Intersecting the resilience and resistance index with the breeding habitat probabilities for GRSG provides information on sage-grouse habitat availability and connectivity, potential for recovery following wildfire, and spatial constraints on recovery (**Figure 5**).

4. Interactions of General and Spatial Resilience With the Predominant Disturbances

The predominant disturbances differ across the sagebrush biome (Chambers et al., 2017a). Invasion of exotic annual grasses and development of grass-fire cycles is a large-scale disturbance in the western part of the biome that is an emerging threat in the eastern part of the biome (Chambers et al., 2019). A large-fire risk assessment for the United States

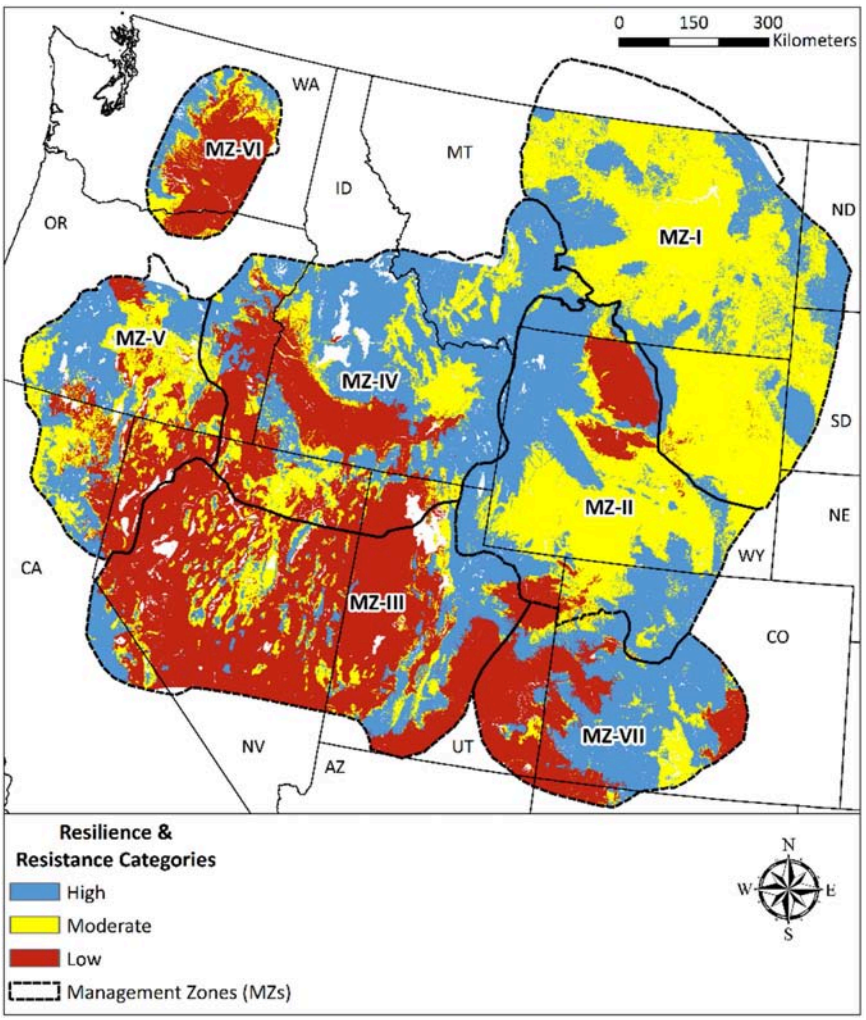


FIGURE 3 | The soil temperature and moisture regime subclasses categorized according to high, moderate, and low resilience to disturbance and resistance to invasive annual grasses (Maestas et al., 2016; Chambers et al., 2017a) overlaid on the sage-grouse Management Zones (Stiver et al., 2006). The soil temperature and moisture regime data are from the USDA Natural Resources Conservation Service, Web Soil Survey (https://websoilsurvey.nrcs.usda.gov).

has been developed from modeled burn probabilities and fire size distributions based on weather data, spatial data on fuel structure and topography, historical fire data, and fire suppression effects (Finney et al., 2011), which was recently updated (Short et al., 2016; **Figure 6**). Intersecting the resilience and resistance index, GRSG breeding habitat probabilities, and large fire risk provides spatially explicit information not only on the likelihood of large fires, but also on likely responses to those fires and effects on high value habitat (**Figure 7**). These maps can be scaled down to local field offices or project areas to facilitate planning designed to locate management strategies where they will be most effective.

5. Management Prioritization and Strategies

The resilience-based framework couples the geospatial data and maps with a sage-grouse habitat resilience and resistance matrix in order to facilitate prioritizing areas for management actions and selecting appropriate strategies (**Table 5**). The matrix is a decision-support tool that allows managers to consider how general resilience may be affecting recovery potential along with how the landscape context and spatial resilience may be influencing capacity to support GRSG populations. The different cells of the matrix are mapped in **Figure 5.** In the matrix and the map, as resilience to disturbance and resistance to invasive annual grasses go from low to high (indicated by the lower to upper rows), the recovery potential increases due to less change from the initial or desired state and a faster rate of recovery. As the probability of sage-grouse habitat goes from low to high within these same systems (indicated by the columns), the capacity to support high value habitat and resources increases as a function of the size and shape of habitat patches and their connectivity.

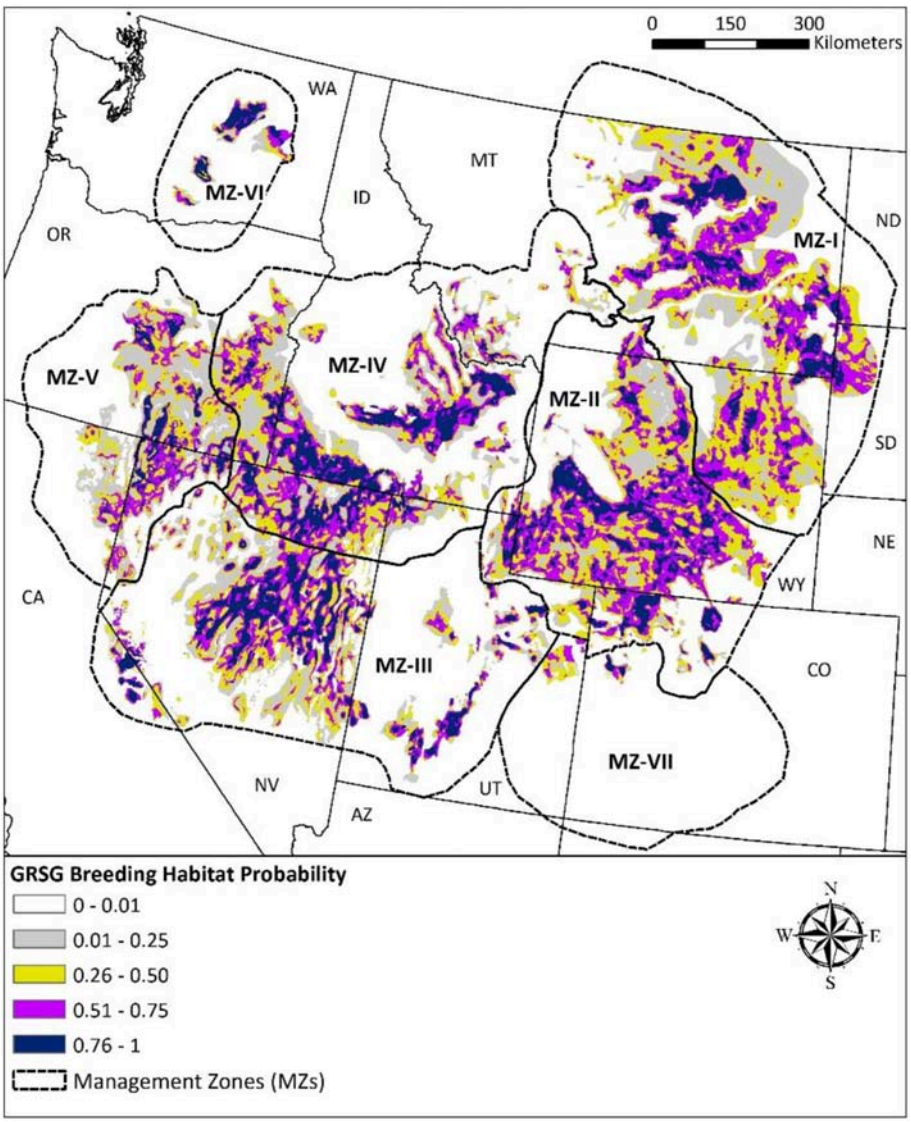


FIGURE 4 | Modeled Greater sage-grouse breeding habitat probabilities based on landscape cover of vegetation, climate, and landform characteristics as well as the type and amount disturbance around breeding sites or leks (within a radius of 6.4 km; Doherty et al., 2016; Chambers et al., 2017a). Sage-grouse Management Zones (Stiver et al., 2006) and Priority Areas for Conservation (USDI FWS, 2015) developed by the States are overlaid.

The general resilience of an area strongly influences its response to both disturbances and management actions (Chambers et al., 2014a,b, 2017b). Areas with high general resilience often have the capacity to return to the prior or a desired state with minimal intervention (**Table 5**, 1A, 1B, 1C). Those with moderate general resilience depend on both the environment and ecosystem attributes and often require more detailed assessments to determine effective management strategies (**Table 5**, 2A, 2B, 2C). Areas with low general resilience are typically among the most difficult to improve and multiple management interventions coupled with preventative measures may be required to obtain a desired state after disturbance (**Table 5**, 3A, 3B, 3C).

The spatial resilience of an area is influenced by (1) resilience to disturbance and resistance to invasive grasses, which influence recovery potentials and the propensity to change states, and (2) anthropogenic developments, which fragment habitats, result in introductions of novel species, and can preclude return to prior states. An area with high sage-grouse breeding habitat probabilities with intact sagebrush ecosystems and high resilience to disturbance and resistance to invasive grasses (**Table 5**, 1C) may have relatively higher spatial resilience over time than one with low resilience and resistance. However, an area with low breeding habitat probabilities due to low landscape cover of sagebrush that has high resilience to disturbance and resistance to invasive grasses (**Table 5**, 1A) may have spatial resilience similar to an area with low resilience to disturbance and resistance to invasive grasses, if anthropogenic development, such as agricultural conversion or oil and gas development, is causing the loss of spatial resilience.

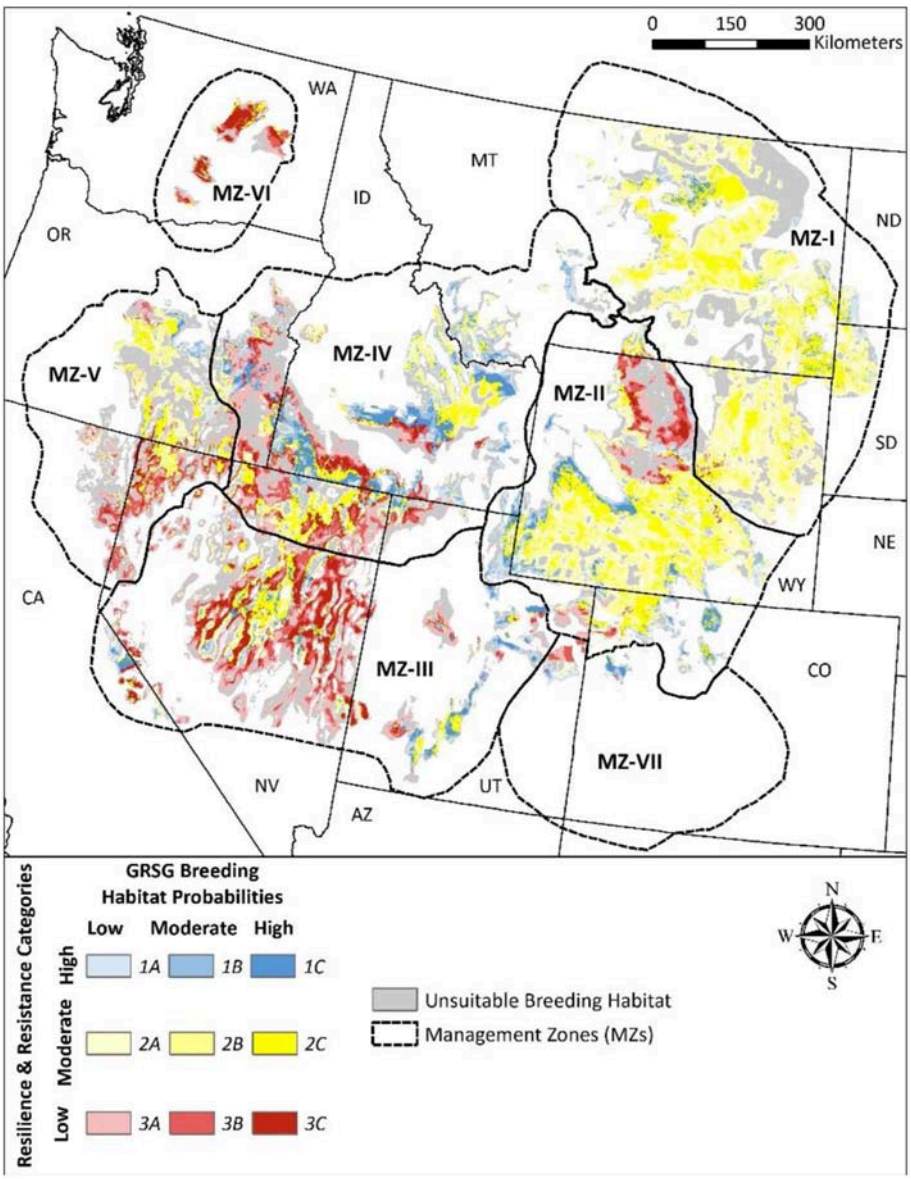


FIGURE 5 | Greater sage-grouse breeding habitat probabilities (Doherty et al., 2016) intersected with resilience and resistance categories developed from soil temperature and moisture regime subclasses (Chambers et al., 2017a). Sage-grouse Management Zones (Stiver et al., 2006) and Priority Areas for Conservation (USDI FWS, 2015) developed by the States are overlaid. This map provides a spatial depiction of the sage-grouse habitat resilience and resistance matrix.

Areas with high sage-grouse breeding habitat probabilities are typically comprised of relatively intact habitat and resource patches, have high spatial resilience, and are high priorities for protective management (**Table 5**, 1C, 2C, 3C; Chambers et al., 2014a, 2017a,b). Regardless of the level of general resilience, protective management can be used in and adjacent to these areas to maintain habitat connectivity and ecological resilience. A diverse set of management strategies can be used including reducing or eliminating disturbances from land uses and development, establishing conservation easements, and utilizing early detection and rapid response approaches for invasive species (USDI, 2016). Areas with high sage-grouse breeding habitat but low general resilience are typically slower to recover following fire and surface disturbances and have lower resistance to invasive annual grasses. Consequently, these areas are at greater risk of habitat loss than areas with moderate to high resilience and resistance and are high priorities for protective management (**Table 5**, 3C, **Figure 7**; Chambers et al., 2014a; Chambers et al., 2017b).

Areas with moderate sage-grouse breeding habitat probabilities and thus spatial resilience often supported a higher proportion of leks in the past and have the capacity for improvement through restoration and other management strategies, particularly if anthropogenic developments are not

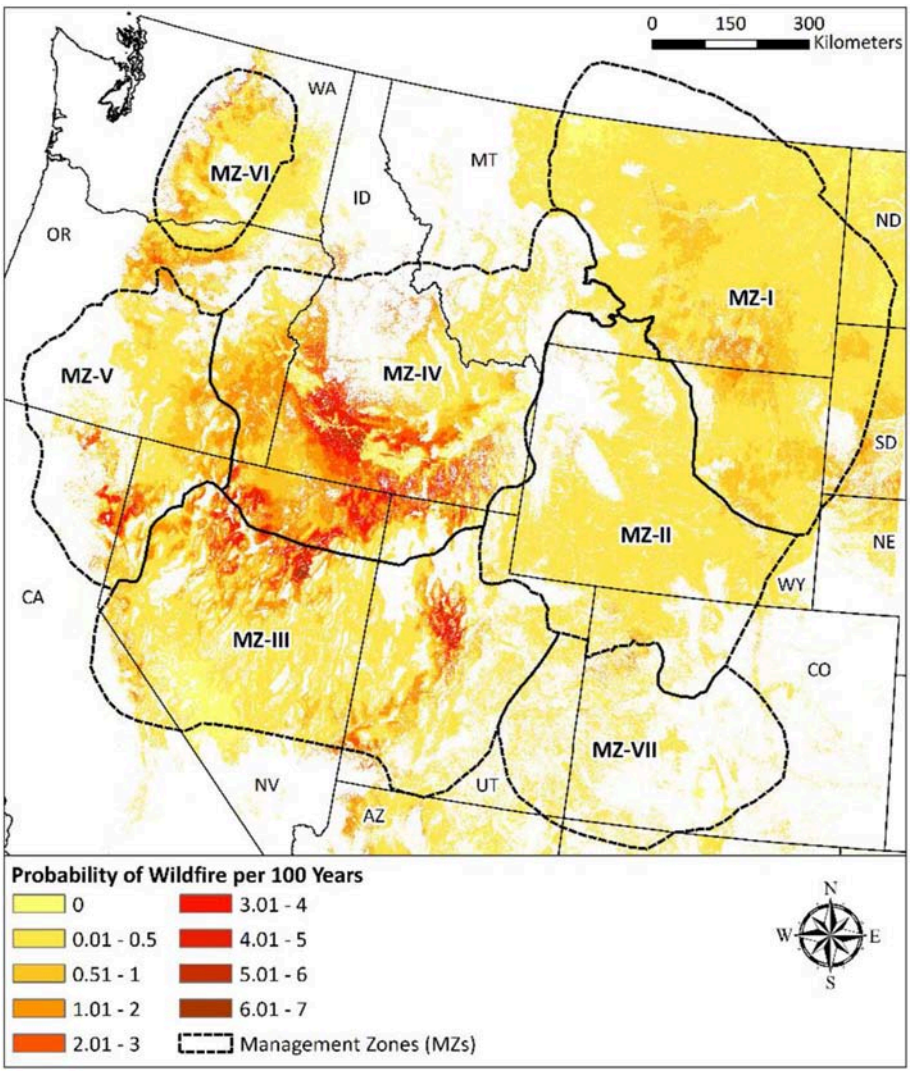


FIGURE 6 | Large fire probability derived by simulating fire ignition and growth using the Fire Simulation (FSim) system (Finney et al., 2011; Short et al., 2016; Chambers et al., 2017a). Sage-grouse Management Zones (Stiver et al., 2006) are overlaid.

causing the loss of resilience (**Table 5**, 1B, 2B, 3B; Knick et al., 2013; Chambers et al., 2014c, 2017b). Management strategies aim to improve resilience of known habitat or resource patches through activities like vegetation manipulation, invasive plant control, or habitat restoration. Habitat restoration can involve passive management, such as changes in levels of human uses like livestock grazing to improve ecological conditions. It can also involve active management such as controlling invading plant species to prevent development of invasive-grass fire cycles, and removing encroaching conifers or seeding or transplanting desirable plant species like sagebrush to increase connectivity. Management strategies may also aim to reduce the risk of altered disturbance regimes, such as wildfires outside of the historical range of variation (**Figure 7**).

Areas with low sage-grouse breeding habitat probabilities are characterized by habitat that may have supported active GRSG leks in the past, but that currently support few leks (**Table 5**, 1A, 1B, 1C). Spatial resilience and thus capacity to support desired resources and habitats has typically been reduced. If land use and development activities such as cropland conversion, energy and mineral development, and urban development are causing the decrease in spatial resilience, then improvement may not be feasible. However, if the area has the capacity to respond to management treatments and has the necessary connectivity to support species populations and allow recolonization, then improvement may still be possible (e.g., Doherty et al., 2016; Ricca et al., 2018). Although managers may decide to invest in improving these types of areas, the degree of difficulty and time frame required usually increases as general resilience decreases and these investments may not be ecologically or cost effective (Calmon et al., 2011); (Chambers et al., 2017a).

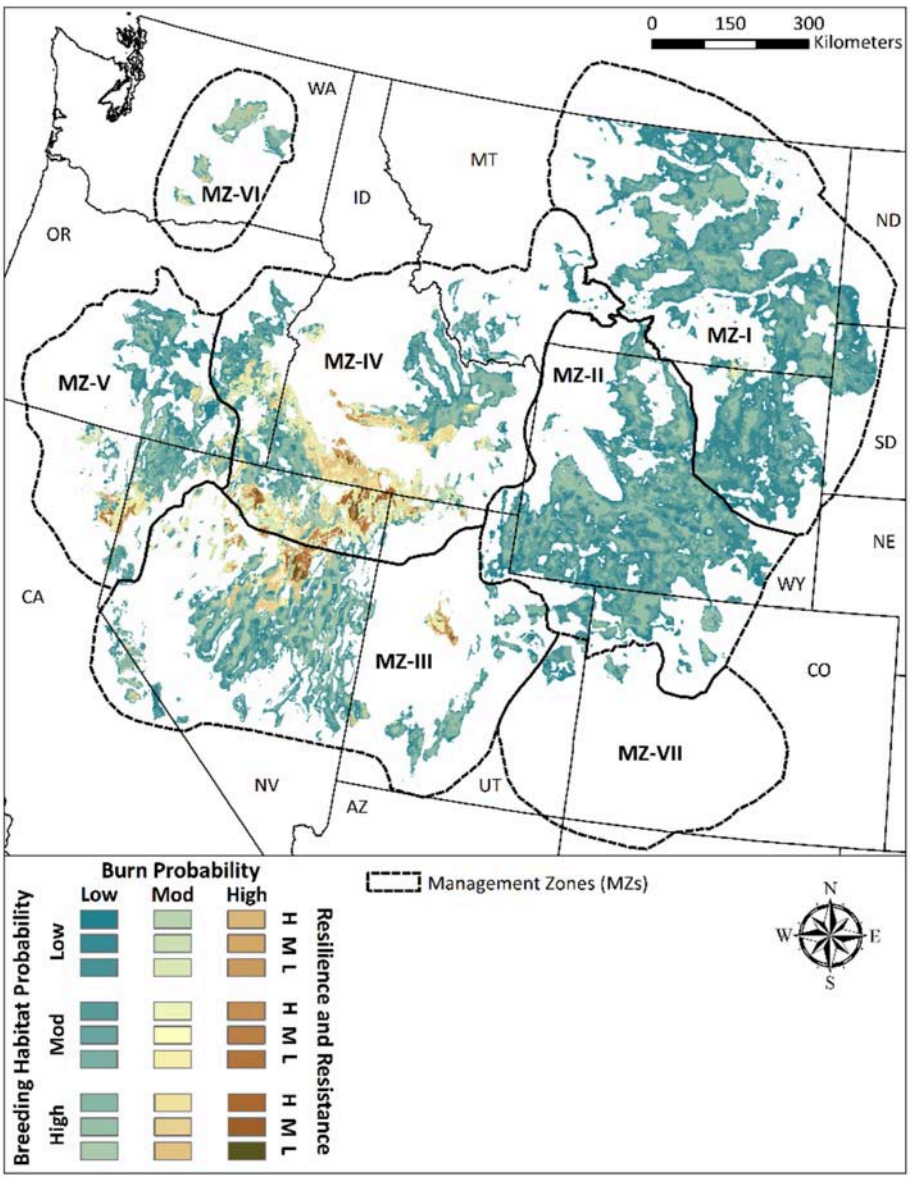
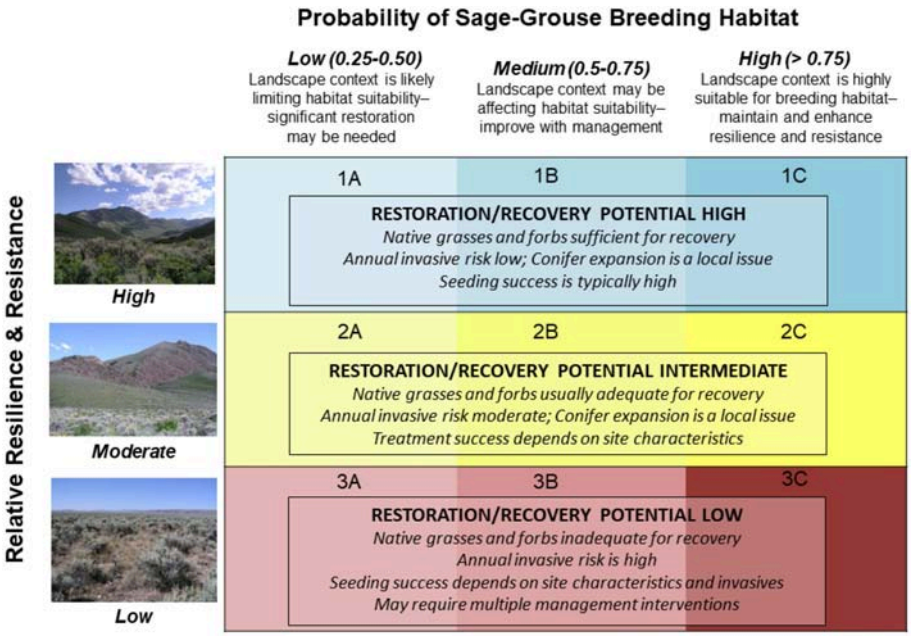


FIGURE 7 | Fire risk map depicting different combinations of sage-grouse breeding habitat probability (Doherty et al., 2016), resilience to disturbance and resistance to invasive annual grasses (Chambers et al., 2017a), and large fire probability (Short et al., 2016). Sage-grouse Management Zones (Stiver et al., 2006) are overlaid. The map identifies sage-grouse habitats that are at highest risk from fire and the relative resilience and resistance of those areas (Chambers et al., 2017a).

In those areas where climate change effects are projected to be severe, management actions may be needed that help ecosystems transition to new regimes (e.g., Millar et al., 2007; Halofsky et al., 2018a,b; Snyder et al., 2018). An understanding of the ecological memory of ecosystems and the role of species functional traits in conveying ecological resilience can be used in a management context to increase adaptive capacity. For example, selecting plant species for restoration with functional traits that allow them to persist in the face of novel disturbances and a warming environment may increase ecological and spatial resilience (Laughlin et al., 2017). In some areas, such as those converted to invasive annual grasses or at risk of conversion, it may be necessary to erode the resilience of a system and help it transition to a more desired alternative regime, or transition to an alternative state may be inevitable given other change (e.g., climate).

Caution is needed to avoid "coerced" resilience or the replacement of natural processes and feedbacks with external anthropogenic inputs. For example, much of the southern Great Plains in the United States has undergone a regime shift from grassland to juniper woodland; many protected grassland areas exist within this now woodland system that are still present due to intensive human intervention. Coerced resilience prevents an alternative state from emerging. If intensive management

TABLE 5 | Sage-grouse habitat resilience and resistance matrix.



Rows illustrate relative resilience to disturbance and resistance to invasive annual grasses (1 = high resilience and resistance; 2 = moderate resilience and resistance; 3 = low resilience and resistance). Relative resilience and resistance are based on soil temperature and moisture subclass regimes and can be related to the dominant sagebrush ecological types (Maestas et al., 2016; Chambers et al., 2017a). Columns illustrate landscape-scale sage-grouse breeding habitat probabilities (low = 0.25 to <0.50); moderate = 0.50 to <0.75; and high = 0.75 to 1.00. The probabilities are based on the probability of areas near leks (within a radius of 6.4 km) providing suitable breeding habitat (Chambers et al., 2016a, 2017a; Doherty et al., 2016). Areas with probabilities of 0.01 to <0.25 are considered unsuitable for breeding habitat. The sage-grouse habitat resilience and resistance matrix provides a decision-support tool for prioritizing areas for management actions and determining effective management strategies. Table adapted from Chambers et al. (2017a).

is stopped, the system may immediately flip to the state of the surrounding landscape (Twidwell et al., 2019), usually because the surrounding landscape has already entered an alternative state. This is a management and philosophical dilemma, as managers are left with three unsatisfactory choices: to maintain such protected areas through perpetual intensive intervention; to try and reverse the broader scale regime shift that occurred; or to let the protected area undergo the regime shift.

Careful assessment of the focal area will always be necessary to determine the relevance of a particular strategy or treatment because ecosystems occur over continuums of environmental conditions, such as effective precipitation, have differing land use histories and species compositions (Johnstone et al., 2016), and may be projected to experience different climate change effects. Using the best available information on the focal ecosystems and species and their responses to management actions can help ensure that treatments are located and strategies implemented in a manner that will meet conservation and restoration objectives. Using structured decision making in the context of adaptive management can help ensure that stakeholders are involved throughout the process.

CONCLUSION

Operationalizing the concepts of general, ecological, and spatial resilience provides the ability to address the effects of ecosystem and anthropogenic disturbances at scales relevant to managers. Evaluating the general and ecological resilience of the ecosystems that comprise landscapes requires developing an understanding of the relationships among the environmental characteristics, ecosystem attributes and processes, and responses to ecosystem and anthropogenic disturbances over time. Evaluating the spatial resilience of landscapes requires understanding the effects of changes in the composition and configuration of landscapes due to ecosystem and anthropogenic disturbances. Integration of resilience concepts in the context of landscapes provides the basis for knowing how ecosystem attributes and processes interact with landscape structure to influence the responses of ecosystems to disturbances and stressors and their capacity to support resources, habitats, and species over time.

Resilience-based management uses a spatially explicit approach, which provides the ability to both quantify and visualize the differences in resilience in relation to focal resources and species and the predominant disturbances. It provides the capacity to determine locations on the landscape where conservation and restoration activities are most likely to be effective and to select the types of management actions that are most likely to succeed. Use of an adaptive management process that uses routine monitoring to adjust management actions in response to changing conditions is a requisite. Effective collaboration among managers, scientists, and stakeholders helps ensure that resilience-based approaches to

management are developed that will be applied to conserve and restore ecosystems. Resilience-based management may require new laws, policies, guidelines, or funding structures in the Anthropocene. It will be most effective when scientific information is used to build consensus in collaborative venues.

AUTHOR CONTRIBUTIONS

JC, CA, and SC conceived the idea and developed the manuscript outline. JC led the writing of the manuscript. CA and SC contributed critically to the draft. All authors gave final approval for publication.

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Climate-Driven Shifts in Soil Temperature and Moisture Regimes Suggest Opportunities to Enhance Assessments of Dryland Resilience and Resistance

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Assessing landscape patterns in climate vulnerability, as well as resilience and resistance to drought, disturbance, and invasive species, requires appropriate metrics of relevant environmental conditions. In dryland systems of western North America, soil temperature and moisture regimes have been widely utilized as an indicator of resilience to disturbance and resistance to invasive plant species by providing integrative indicators of long-term site aridity, which relates to ecosystem recovery potential and climatic suitability to invaders. However, the impact of climate change on these regimes, and the suitability of the indicator for estimating resistance and resilience in the context of climate change have not been assessed. Here we utilized a daily time-step, process-based, ecosystem water balance model to characterize current and future patterns in soil temperature and moisture conditions in dryland areas of western North America, and evaluate the impact of these changes on estimation of resilience and resistance. Soil temperature increases in the twenty-first century are substantial, relatively uniform geographically, and robust across climate models. Higher temperatures will expand the areas of mesic and thermic soil temperature regimes while decreasing the area of cryic and frigid temperature conditions. Projections for future precipitation are more variable both geographically and among climate models. Nevertheless, future soil moisture conditions are relatively consistent across climate models for much of the region. Projections of drier soils are expected in most of Arizona and New Mexico, as well as the central and southern U.S. Great Plains. By contrast, areas with projections of increasing soil moisture include northeastern Montana, southern Alberta and Saskatchewan, and many areas dominated by big sagebrush, particularly the Central and Northern Basin and Range and the Wyoming Basin ecoregions.

In addition, many areas dominated by big sagebrush are expected to experience pronounced shifts toward cool season moisture, which will create more area with xeric moisture conditions and less area with ustic conditions. In addition to indicating widespread geographic shifts in the distribution of soil temperature and moisture regimes, our results suggest opportunities for enhancing the integration of these conditions into a quantitative framework for assessing climate change impacts on dryland ecosystem resilience and resistance that is responsive to long-term projections.

Keywords: aridification, big sagebrush ecosystems, cheatgrass, climate change, drought, ecological transformation, vulnerability

INTRODUCTION

Global change, particularly altered disturbance regimes, biological invasions, and long-term climatic shifts, represent growing challenges for policy makers, and natural resource managers working to sustain ecosystem services (Glick et al., 2010). Among the most important applied information needs to maximize the ability of resource managers to cope with these changes is reliable understanding of geographic patterns in ecosystem vulnerability to climate change and subsequent impacts on ecological resilience (**Box 1**) to disturbance and other stressors (Briske et al., 2015). Decision makers need a quantitative, systematic way to recognize how locations differ in their expected response to changes in both climate and disturbances. This information would enable efficient prioritization and resource allocation by identifying areas where management activities can increase the adaptive capacity of ecosystems and minimize adverse impacts. It would also identify those areas where important changes in climate are expected and management activities need to focus on assisting ecosystems in transitioning to the new conditions (Millar et al., 2007; Snyder et al., 2018).

The need for insights about geographic patterns of climate vulnerability is especially pronounced in dryland regions, where degradation has been widespread and many ecosystems are heavily dependent on moisture that is acquired in the soil profile (Huang et al., 2017). Persistent land degradation due to combinations of land use, disturbance, and biological invasions, has emerged as one of the most pressing contemporary management challenges in dryland regions (Herrick et al., 2012). The simultaneous increase in the abundance of degraded land and growing land use pressure often impede efforts to sustain or restore dryland ecosystems (Kildisheva et al., 2016). In addition, because rising temperatures are among the most consistent projected aspects of climate change, and higher temperature exacerbates aridity, dryland regions may be especially impacted by climate change (Huang et al., 2017). However, plants in dryland environments respond primarily to soil moisture, not precipitation (Noy-Meir, 1973). As a result, accurately projecting the magnitude, potential implications, and uncertainty of changes in drought stress experienced by dryland ecosystems in response to rising temperature and altered future precipitation patterns is complicated (Wang et al., 2012). Because climatic conditions, edaphic properties, and vegetation feedbacks interact to influence moisture availability, dryland ecosystem vulnerability to climate change and ecological resilience to disturbance are highly heterogeneous in both space and time. This heterogeneity represents a substantial challenge to developing geographically appropriate management strategies that prevent degradation and promote recovery from disturbance.

In the dryland ecosystems that characterize much of western North America, long-term environmental conditions can provide useful insights into ecological resilience to disturbance and resistance to invasive species (Chambers et al., 2014a, 2019a,b). Recent work has applied soil characteristics to describe geographic patterns of disturbance resilience and invasion resistance, specifically cheatgrass (*Bromus tectorum*), at regional to site scales (Chambers et al., 2016, 2017a,b; Maestas et al., 2016). Specifically, soil temperature and moisture regimes, based on soil taxonomy and mapped by the National Cooperative Soil Survey, were used because they integrate the combined effects of temperature and precipitation to

BOX 1 | Ecological vulnerability, resilience, and resistance.

Vulnerability to climate change: The degree to which a system is susceptible to, and unable to cope with, adverse effects of climate change, including climate variability, and extremes. Vulnerability is a function of climate *exposure*, the magnitude of expected change in climate mean and variability; *sensitivity*, the potential ecological impact of changing climate; and *adaptive capacity*, the ability of a system to maintain critical composition and function as climate changes (Glick et al., 2010; Stein et al., 2014).

Ecological resilience: The amount of change needed to change an ecosystem from one set of processes and structures to a different set of processes and structures or the amount of disturbance that a system can withstand before it shifts into a new regime or alternative stable state (Holling, 1973). In the applied context here, resilience describes the capacity of an ecosystem to regain its fundamental structure, processes, and functioning (or remain largely unchanged) despite stresses and disturbances (Hirota et al., 2011; Chambers et al., 2014a; Seidl et al., 2016).

Ecological resistance: The ability of an ecosystem to stay essentially unchanged despite the presence of disturbances and stressors (Grimm and Wissel, 1997). In the applied context here, resistance describes the attributes and processes of an ecosystem that influence the potential population growth and eventual dominance by an invading species (D'Antonio and Thomsen, 2004).

characterize overall patterns of soil moisture availability for plant communities and represent estimates of long-term, typical conditions (Soil Survey Staff, 2014). Potential resilience and resistance (R&R) varies across environmental gradients and among ecological types and ecological sites (Chambers et al., 2014a). To facilitate broad-scale analyses of resilience and resistance, the dominant ecological types in the sagebrush range were identified and their soil temperature and moisture regime determined. Then resilience and resistance categories were assigned to each ecological type based on available ecological site descriptions and expert knowledge. Soil survey spatial and tabular data were aggregated according to soil temperature and moisture regime and moisture subclass (Maestas et al., 2016). A simplified index of relative resilience and resistance was generated by assigning each soil temperature and moisture regime/moisture subclass to one of three categories (high, moderate, and low) based on the ecological type descriptions and expert input. These simplified categories have provided a useful framework for ecologically-based resource allocation and determination of appropriate management strategies across scales (Maestas et al., 2016; Chambers et al., 2017a,b).

As climatic conditions change, soil temperature and moisture conditions will also change. Soil temperature and moisture regimes are defined by criteria that indicate how temperature and moisture conditions differ among regimes (Soil Survey Staff, 2014). However, current geographic databases for both temperature and moisture regimes are derived from soil surveys that use qualitative approaches, for example indicator plant species, to map the geographic distribution of regimes. As a result, these survey-based methods do not lend themselves to a quantitative assessment of the future distribution of soil temperature and moisture regimes. Projections of future regimes will require a process-based approach in which regimes are systematically linked to driving climatic and edaphic conditions.

Because soil temperature and moisture regimes are currently being incorporated into natural resource planning and management, developing projections for future changes is an important step toward quantifying and understanding uncertainty around climate change impacts. Our overall goal was to assess how projected changes in climate will alter soil temperature and moisture conditions in drylands of western North America. We simulated soil temperature and moisture conditions for current climate, and for future climate represented by all available climate models at two time periods during the twenty-first century. We used the results to: (1) quantify the direction and magnitude of expected changes in several measures of soil temperature and soil moisture, including the key variables used to distinguish the regimes used in the R&R categories; (2) assess how these changes will impact the geographic distribution of soil temperature and moisture regimes; and (3) explore the implications for using R&R categories for estimating future ecosystem resilience and resistance.

METHODS

Study Area

We quantified soil temperature and moisture conditions in dryland areas of the U.S. and Canada where the ratio of mean annual precipitation to potential evapotranspiration was <0.6. We simulated conditions on a 10-km resolution grid, resulting in 58,694 cells for the entire dryland extent. Because resilience and resistance concepts are widely developed for big sagebrush ecosystems, we describe results for resilience and resistance metrics only within the Greater Sage-grouse Management Zones (Manier et al., 2013), an area represented by 16,111 cells (**Figure S2.1**).

Soil Temperature and Moisture Variables Examined

We quantified current and future conditions for two soil temperature variables (**Figure 1**) that define soil temperature regimes as defined by the National Cooperative Soil Survey (Soil Survey Staff, 2014): mean annual soil temperature at 50 cm depth (hereafter T_{ANN50}), and mean summer (June–August) temperature at 50 cm depth (T_{SUM50}). Conditions with $T_{ANN50} < 0$ are classified as other (primarily permafrost), while increments of 8°C separate the remaining soil temperature regimes, with the

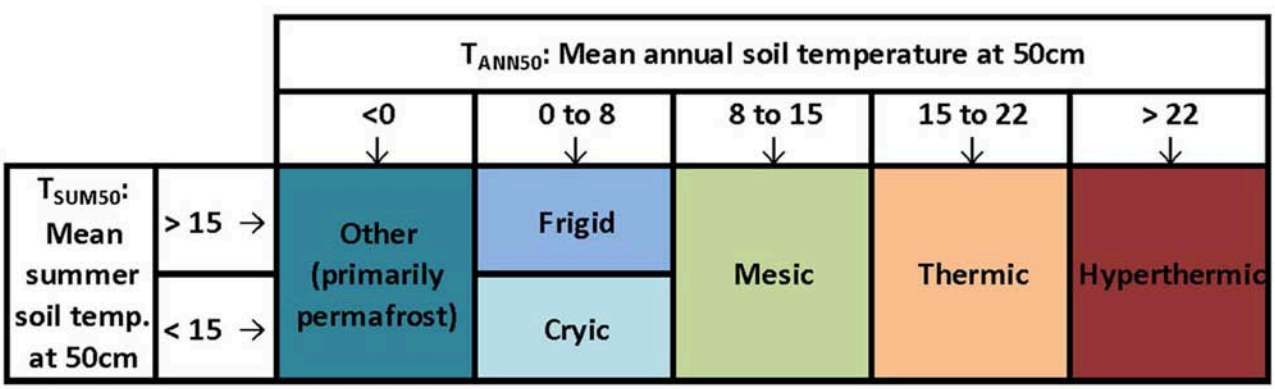

FIGURE 1 | Simplified relationships between soil temperature regimes (colors) and primary criteria for distinguishing the regimes. See text for descriptions of criteria.

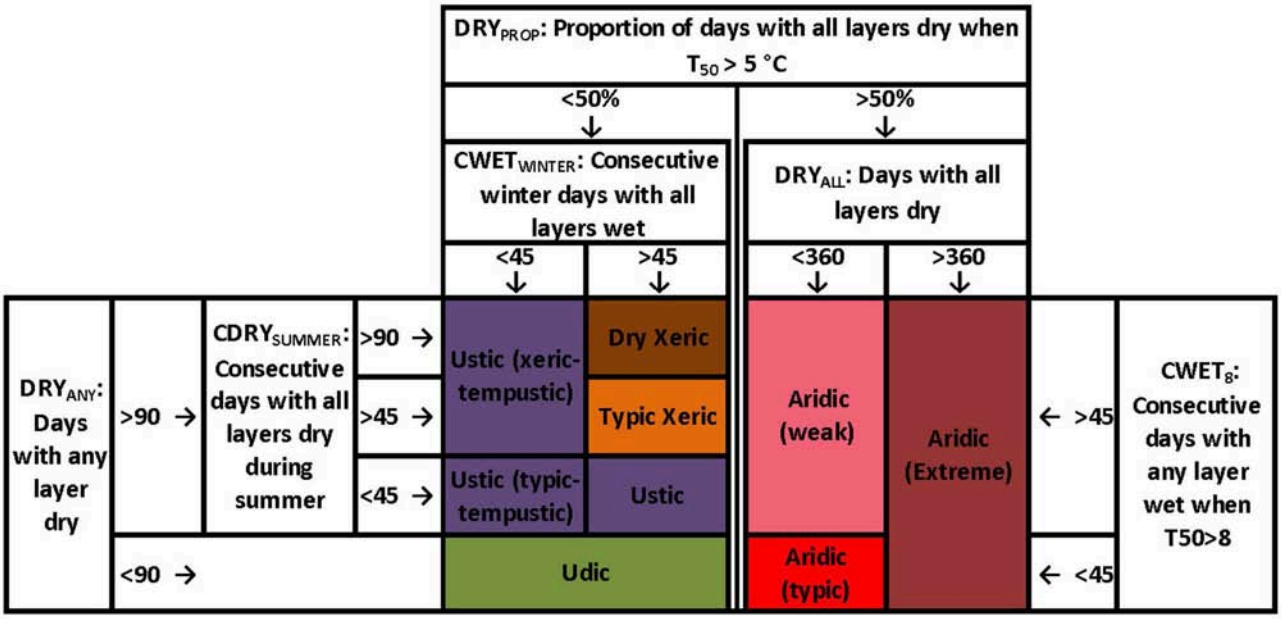

FIGURE 2 | Simplified relationships among soil moisture regimes (colors) and primary criteria for distinguishing the regimes. See text for descriptions of criteria.

exception of Frigid and Cryic, which are further distinguished from one another by T_{SUM50}: soils with $T_{SUM50} > 15°C$ are characterized as Frigid, while Cryic regimes are defined by $T_{SUM50} < 15°C$.

Soil moisture regimes are defined (Soil Survey Staff, 2014) by combinations of several variables (**Figure 2**) describing the frequency and seasonality of wet (>−1.5MPa) soil conditions within the moisture control section (MCS: soil layers with depth ranging from 10 to 30 cm for fine textures to 30–90 cm for coarse textures; Soil Survey Staff, 2014). We focus here on the three most important variables for differentiating among the moisture regimes in drylands of western North America: DRY_{PROP}, $CWET_{WINTER}$, and $CDRY_{SUMMER}$. First, the proportion of days that all layers within the MCS are dry when soil temperature at 50 cm > 5°C (DRY_{PROP}) provides an overall measure of aridity and distinguishes Aridic from all other regimes. The other two variables represent seasonal patterns of moisture availability in non-aridic areas, and distinguish between Ustic (seasonally summer moist) and Xeric (seasonally winter moist) conditions. These are the number of consecutive days with all MCS layers wet during the winter ($CWET_{WINTER}$: winter here defined as the 4 months following the winter solstice), and the number of consecutive days with all MCS layers dry during the summer ($CDRY_{SUMMER}$: summer defined as the 4 months following the summer solstice). In the **Supplementary Materials**, we also provide results for three other soil moisture variables that relate to the soil moisture regimes but are not as influential for the western U.S: DRY_{ALL}, $CWET_8$, and DRY_{ANY} (**Figure 2**). Two variables distinguish among Aridic-weak, Aridic-typic, and Aridic-extreme regimes: the number of days with all MCS layers dry (DRY_{ALL}), and the number of consecutive days with any layer wet when soil temperature at 50 cm depth (T_{50}) is > 8°C ($CWET_8$). The last variable, the number of days when any soil layer in the MCS is dry (DRY_{ANY}), differentiates wetter Udic conditions from Xeric and Ustic conditions.

Ecohydrological Modeling

Current and future patterns of soil temperature and moisture were assessed using the SOILWAT2 ecosystem water balance model (Schlaepfer and Andrews, 2018; Schlaepfer and Murphy, 2018). SOILWAT2 (described in **Appendix 5**) is a daily time step, multiple soil layer, process-based, simulation model of ecosystem water balance that has been applied in numerous dryland ecosystems (Bradford and Lauenroth, 2006; Lauenroth and Bradford, 2006; Schlaepfer et al., 2012, 2017; Bradford et al., 2014a,b; Tietjen et al., 2017). Inputs to SOILWAT2 include daily temperature and precipitation, mean monthly relative humidity, wind speed and cloud cover, monthly vegetation (live and dead biomass, litter, and active root profile) and site-specific properties of each soil layer. For each 10 km cell, we estimated soil temperature and moisture conditions for four different soil types. We simulated conditions using site-specific soils (**Figure S4.1**), based on data for each soil layer (sand %, clay %, volume of gravel, bulk density, soil depth) for each grid cell from the aggregated databases NRCS STATSGO (1 km2 grids; Miller and White, 1998) within the United States and ISRIC-WISE v1.2 (5-arcmin; Batjes, 2012) for areas in Canada. Results from these site-specific simulations are the primary focus of the manuscript. However, to provide insight into the influence of divergent soil conditions, we also simulated conditions in three fixed soil types that included a clay loam (27% sand, 35% clay, 38% silt), a sandy loam (66% sand, 9% clay, 25% silt), and a silt loam (16% sand, 9% clay, 75% silt). Results from these fixed soil simulations are presented in **Appendix 3**. For each cell, we estimated the

relative composition of C_3 and C_4 grasses and woody plants as well as monthly biomass, litter, and root depth distributions from climate conditions (e.g., relatively more C4 grasses in warm areas with high summer precipitation, more C3 grasses in cooler areas with winter precipitation, and more shrubs in cool-dry areas with winter precipitation; Paruelo and Lauenroth, 1996) using methods described in Bradford et al. (2014b) and Palmquist et al. (2016a).

Climate Scenarios and Data Sources

Climate data layers included both current and future climatic conditions developed for a 10-km resolution grid across western North America. We used NCEP/CFSR products (Saha et al., 2010) for current climate conditions (1980–2010) by extracting daily maximum and minimum temperature (2 m above ground) and precipitation from the 6-hourly T382 products (U. S. National Centers for Environmental Prediction, 2010a,b). For future conditions, we extracted climate conditions as monthly time-series for two time periods, 2020–2050 and 2069–2099, from 1/2-degree downscaled and bias-corrected products of the fifth phase of the Climate Model Intercomparison Project (Taylor et al., 2012) (CMIP5). We extracted data from all available general circulation models (GCMs) for two representative concentration pathways (RCP4.5–37 GCMs; RCP8.5–35 GCMs) (Moss et al., 2010). We obtained data from the "Downscaled CMIP3 and CMIP5 Climate and Hydrology Projections" archive (Maurer et al., 2007) at http://gdo-dcp.ucllnl.org/downscaled_cmip_projections/. We combined historical daily data (NCEP/NFSR) with monthly GCM predictions of historical and future conditions with a hybrid-delta downscaling approach to obtain future daily forcing (Hamlet et al., 2010; Tohver et al., 2014).

Soil Regimes and Resilience/Resistance Categorization

The National Cooperative Soil Survey has developed an algorithm, described in Soil Survey Staff (2014). We implemented the soil temperature and moisture regime logic in conjunction with the SOILWAT2 model, as described in the vignette "SoilMoistureRegimes_SoilTemperatureRegimes" of the R package rSOILWAT2 (Schlaepfer and Murphy, 2018). The basic criteria used to determine soil temperature and moisture regimes are illustrated in **Figures 1**, **2**, respectively. We evaluated conditions during "normal" years, which are defined as having annual temperature, annual precipitation, and monthly precipitation for at least 8 of the 12 months within one standard deviation of long-term mean conditions (Soil Survey Staff, 2014). For each grid cell, we examined the specific soil temperature and moisture variables described above during normal years to determine the appropriate soil temperature and moisture regime, based on the criteria summarized in **Figures 1**, **2**. Logic for assigning resilience and resistance classes based on soil temperature and moisture regimes have been developed for various regions (Chambers et al., 2014c, 2016; Maestas et al., 2016). We synthesized these categorizations (**Figure S2.4**) and applied them to assign current and potential future ecosystem resilience and resistance. We only evaluated resilience and resistance in big sagebrush dominated ecosystems, which is where assessments of the R & R categories have been developed. These systems are defined here as the extent of the greater sage-grouse management zones (**Figure S2.1**), which are important conservation planning units in western North America (Manier et al., 2013).

Ensemble Approach

We calculated all variables and resulting regimes under historical climate conditions and for each GCM under both RCPs and for both time periods. We present results for the median GCM within each RCP and time period, and identify areas where >90% of the GCMs within each RCP and time period (i.e., >33 GCMs under RCP4.5 and >31 under RCP8.5) agree on either the direction of change in continuous temperature or moisture variables, or agree on the regime categorization. All analyses on simulation output variables were performed in R version 3.3.2 (R Core Team, 2016).

RESULTS

Averaged across our entire study region, the median climate model indicated near-term (2020–2050) mean annual air temperature increases of ∼1.7°C under RCP8.5 (ranges described here represent 10–90% of GCMs, which in this case was 1.2–2.4°C) and 1.5°C under RCP4.5 (0.9–2.0 °C). In the long-term (2070–2100), temperature increases grow to 4.9°C for RCP8.5 (3.5–6.4°C) and 2.6°C for RCP4.5 (1.6–3.7°C). For both the near-term and long-term projections, areas where more than 90% of the GCMs indicated temperature increases were ubiquitous, and the magnitude of the increase in temperature was reasonably consistent across these North American drylands (**Figure S1.1**). By contrast, projections for changes in annual precipitation varied substantially both geographically and among GCMs (**Figure S1.2**). Under RCP8.5, average near-term precipitation change across the study region for the median GCM is +15 mm with 10–90% of GCMs ranging from of −23 mm to +56 mm. In the long-term, average precipitation change for the median GCM was +22 mm (−36 mm to +89 mm). Locations where >90% of GCMs agree in the direction of change in mean annual precipitation included only areas with projected precipitation increases and were confined in the near term to small areas in Wyoming and the northwest portion of the study area (**Figure S1.2**). In the long term, areas with robust projections for increasing precipitation are more widespread but still confined to the northern portion of North American drylands.

Soil Temperature

Averaged across the study area, mean annual soil temperature at 50 cm depth (T_{ANN50}) increased for all future climate scenarios (**Figure 3** and **Figure S1.4**). T_{ANN50} increase in the near-term (2020–2050) averaged 1.25°C for the median GCM under RCP8.5 (10–90% of GCMs: 0.7°–1.9°C) and 1.1°C under RCP4.5 (0.4–1.7°C). For the long-term (2070–2100), average T_{ANN50} was projected to increase to 3.6°C for the RCP8.5 median GCM (2.3°-5.0°C), and 1.9°C under RCP4.5 (GCM range 0.9°–3.0°C, **Figure S1.4**). Summer soil temperature at 50 cm depth (T_{SUM50}) increased under all future scenarios

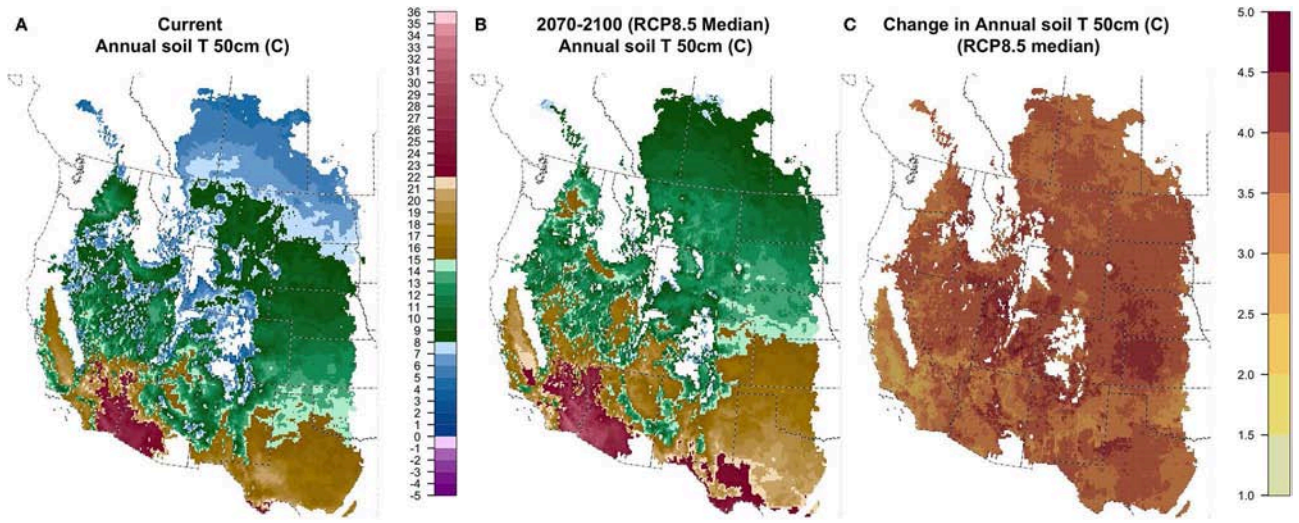

FIGURE 3 | Current **(A)**, future (**B**; 2070–2100; RCP8.5 median model), and change **(C)** in $T50_{ANN}$: mean annual soil temperature (°C) at 50 cm depth.

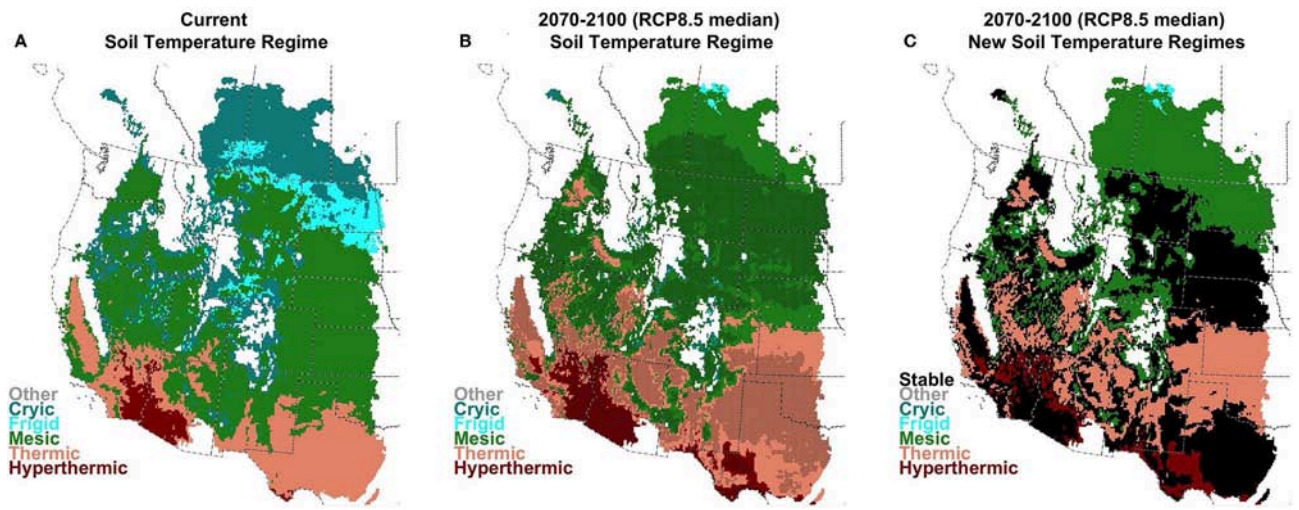

FIGURE 4 | Current **(A)**, future (**B**; 2070–2100; RCP8.5 median model), and change **(C)** in soil temperature regimes. Stippling indicates areas where >90% of climate models agree on the assignment of the regime under future conditions.

(**Figure S1.5**), with slightly larger magnitudes and stronger geographic patterns than T_{ANN50}. These temperature increases supported substantial shifts in the geographic distribution of soil temperature regimes (**Figure 4** and **Figure S1.6**). The extent of cooler Cryic and Frigid regimes, currently representing 31% of the region, were projected to represent only 19% in the near-term for RCP8.5 (21% for RCP4.5), and <2% in the long-term for RCP8.5 (14% for RCP4.5). Thermic and Hyperthermic regimes, currently found only in the southern portion of the region, expanded from 21% of the region to 28% in the near-term for RCP8.5 (27% for RCP 4.5) and 41% in the long-term (32% for RCP4.5). Mesic soil temperatures increased modestly, from 48% of the region currently to 53% in the near-term (52% for RCP4.5) and 58% in the long-term (54% for RCP4.5). Especially for RCP8.5 and the long-term, Thermic and Hyperthermic regimes expanded in the southern and middle portion of the study area, at the expense of the Mesic regime, which shifted northward.

Soil Moisture Overall Aridity

Aridic soil moisture regimes are distinguished from other regimes by $DRY_{PROP} > 50\%$, where DRY_{PROP} is the proportion of warm days ($T_{50} > 5$) that have entirely dry soils (warm and dry days divided by total warm days; **Figure 2**). For the median GCM, we found that future climate conditions promoted increases on average in both the number of warm days (**Figure S1.7**) and the number of warm and dry days (**Figure S1.8**). Near-term projections for the median GCM suggest an increase of 16 warm days for RCP8.5 (10–90% of GCMs: 9–26 days) and 14 days for RCP4.5 (6–22 days). Long-term projections indicated 45 more

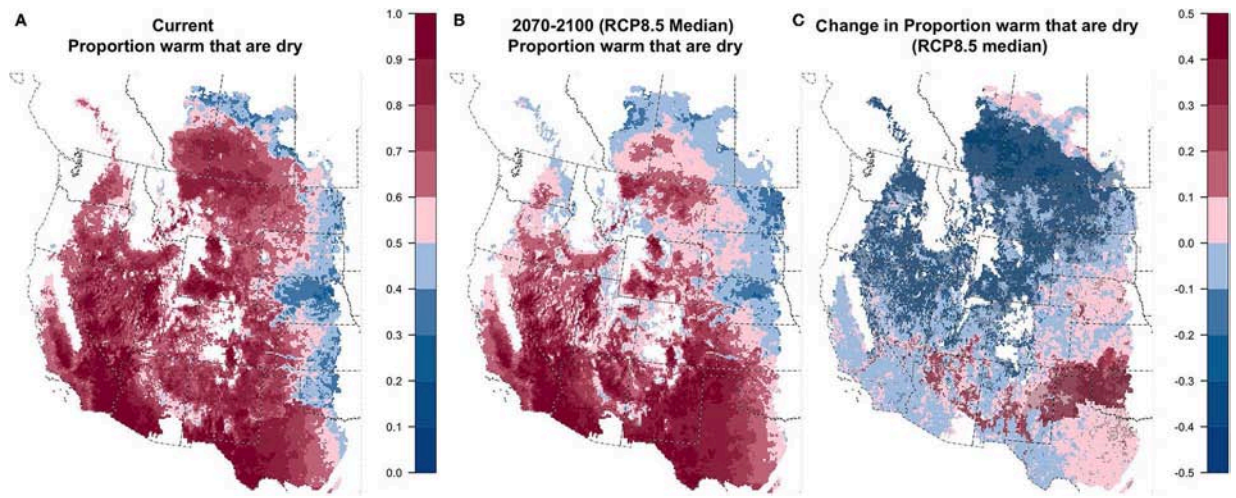

FIGURE 5 | Current **(A)**, future (**B**; 2070–2100; RCP8.5 median model), and change **(C)** in DRY_{PROP}: proportion of days with all soil layers dry when $T_{50} > 5°C$.

warm soil days per year for the median GCM for RCP8.5 (30–61 days) and 25 more days for RCP4.5 (12–39 days). Projections for increases in days that are both warm and dry generally increased slightly slower than warm days. Projected increases in warm-dry days for the median GCM are only 6 (10–90% of GCMs: −9 to 21) for both RCP8.5 and RCP4.5, while long-term increases are 20 days for RCP8.5 (−2 to 47 days) and 11 days for RCP4.5 (−7 to 30 days). In most parts of these drylands, particularly the central and northern portions of the region, the projected increase in warm days exceeded the increase in warm and dry days (**Figure S4.2**), resulting in lower DRY_{PROP} (**Figure 5** and **Figure S1.9**). In other limited portions of the region, notably the central and southern Great Plains and portions of the Arizona-New Mexico highlands, DRY_{PROP} was projected to increase in the future as the number of warm and dry days outpaces the number of warm days. For locations meeting the overall criteria to be considered aridic ($DRY_{PROP} > 50\%$), weak aridic is characterized by having >45 consecutive hot days ($T_{50} > 8$) with any soil layer wet, a condition that increased in prevalence across most of the region (**Figure S1.10**) probably because the number of hot days was greater in the future. Extreme aridic regimes are distinguished by having >360 days with all soil layers dry. Although the number of days with all dry soils increased across some portions of the region (**Figure S1.11**), very few areas had more than 360 entirely dry days under either current or future conditions.

Soil Moisture Seasonality

Very little of the study region has <90 days with any soil layer dry, which is necessary to qualify as the relatively wet Udic soil moisture regime (**Figure S1.12**). As a result, moisture patterns in the non-arid areas are defined (**Figure 2**) by either winter soil moisture availability (Xeric) or summer soil moisture availability (Ustic). Winter moisture is quantified by $CWET_{WINTER}$, the number of consecutive winter days with all soil layers wet. Projections for $CWET_{WINTER}$ indicated increasing winter moisture over most of the northwest and north-central portions of our region and decreases in much of the southeastern area, with broad areas where 90% of GCMs agreed on the direction of change (**Figure 6** and **Figure S1.13**). Summer moisture availability is quantified by the number of consecutive summer days when all soil layers are dry ($CDRY_{SUMMER}$), which was projected to change only modestly with both increases and decreases expected (**Figure 7** and **Figure S1.14**). The exception was the eastern portion of our study area, covering much of the central Great Plains, where $CDRY_{SUMMER}$ was projected to increase in >90% of GCMs and median increases were >20 days over large areas, particularly for RCP8.5.

Climate-driven changes in the metrics related to aridic soil moisture regimes, and to the seasonality of soil moisture availability for wetter locations combined to alter the geographic patterns of soil moisture regimes within drylands of western North America. However, the changes differed substantially among regions (**Figure 8** and **Figure S1.15**). Throughout much of the northern portion of these drylands, decreasing proportion of warm days that have dry soils (as quantified by DRY_{PROP}) resulted in less area with an aridic soil moisture regime. Aridic soil moisture regimes are currently found across 43% of this region, and that proportion is projected to decrease in the near-term to 34% under RCP8.5 (GCM range: 23–52%) and 36% for RCP4.5 (24–53%). In the long term, aridic regimes decrease to 30% for RCP8.5 (19–47%) and 33% for RCP4.5 (21–50%). In the intermountain portions of these areas, characterized by the Greater Sage-grouse Management Zones (**Figure S2.3**), areas with aridic regimes were replaced with xeric regime classifications, with the exception of the northern Great Plains where aridic-classified areas were replaced with ustic soil moisture classifications. Changes in the southern portions of these drylands were more variable, although increasing aridity was projected in northeast New Mexico and the Texas and Oklahoma panhandles (**Figure 8**).

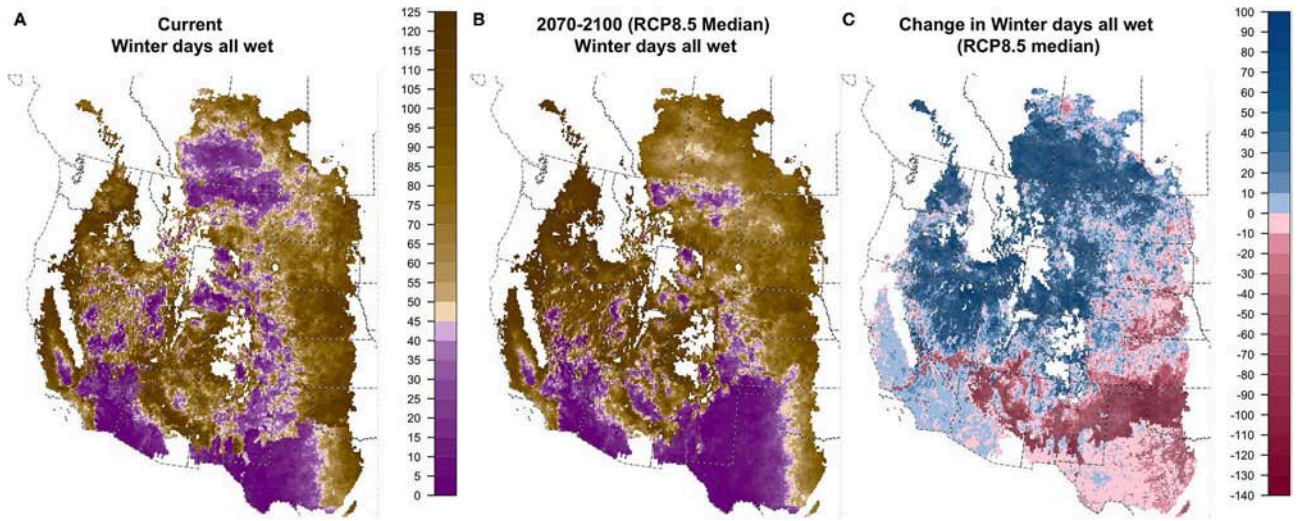

FIGURE 6 | Current **(A)**, future (**B**; 2070–2100; RCP8.5 median model), and change **(C)** in $CWET_{WINTER}$: consecutive winter days with all soil layers wet.

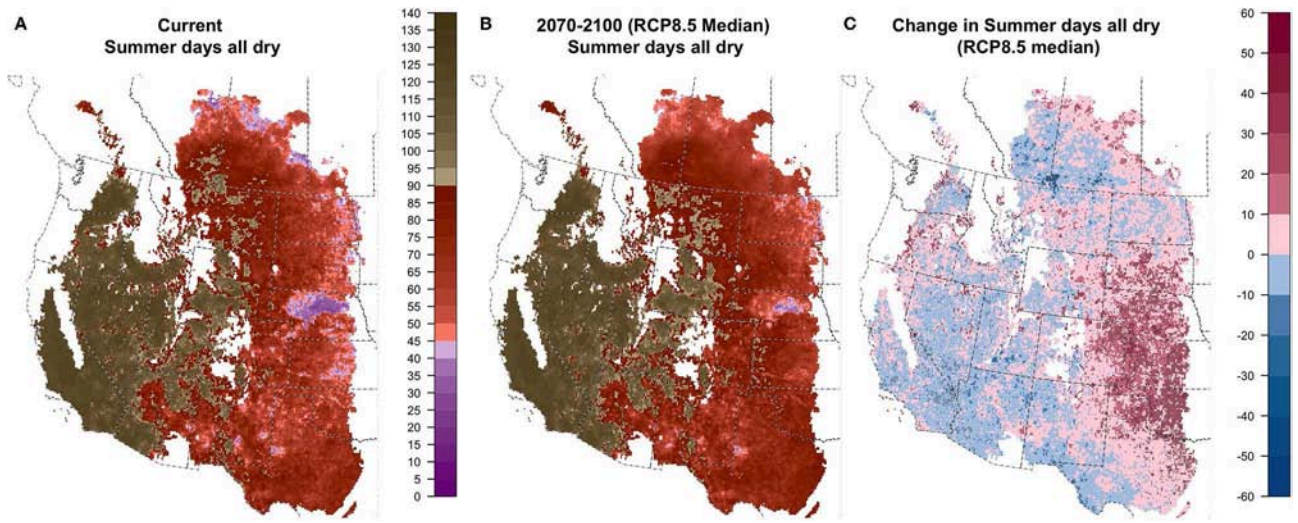

FIGURE 7 | Current **(A)**, future (**B**; 2070–2100; RCP8.5 median model), and change **(C)** in $CDRY_{SUMMER}$: consecutive summer days with all layers dry.

Resilience and Resistance in Big Sagebrush Dominated Areas

With only very minor regional variation, high R&R are linked to cold and wet conditions, while low R&R are linked to hot and dry conditions (**Figure S2.4**). Our results examining the effect of climate change on soil temperature and moisture regimes implies decreasing abundance of both low and high R&R, and an associated increase in moderate R&R, especially in the long-term for RCP8.5 (**Figures S2.5**, **S2.6**). Rising soil temperatures create few areas with Cryic and Frigid temperature regimes (**Figure S2.2**), and thereby reduce the extent of areas categorized as high R&R from 42% of the region under current conditions to 23% in the long-term under RCP8.5 (37% under RCP4.5; **Figures 9**, **10**, and **Figures S2.5**, **S2.6**). Many of these areas become moderate-low R&R, which increases from 2% of the region currently to 21% in the long-term under RCP 8.5 (11% under RCP 4.5). Simultaneously, as fewer locations meet the criteria defined for the aridic soil moisture regime (described above), areas categorized as low R&R decrease from 16% currently to 3% in the long term under RCP8.5 (8% under RCP4.5). Moderate R&R areas increase from 38% currently to 53% in the long-term under RCP8.5 (44% under RCP4.5; **Figure 9** and **Figures S2.5**, **S2.6**).

Variability Among Soil Types

Results for the three fixed soil types that we examined in addition to the site-specific soils indicated that soil temperature conditions are relatively unimpacted by soil texture, while soil

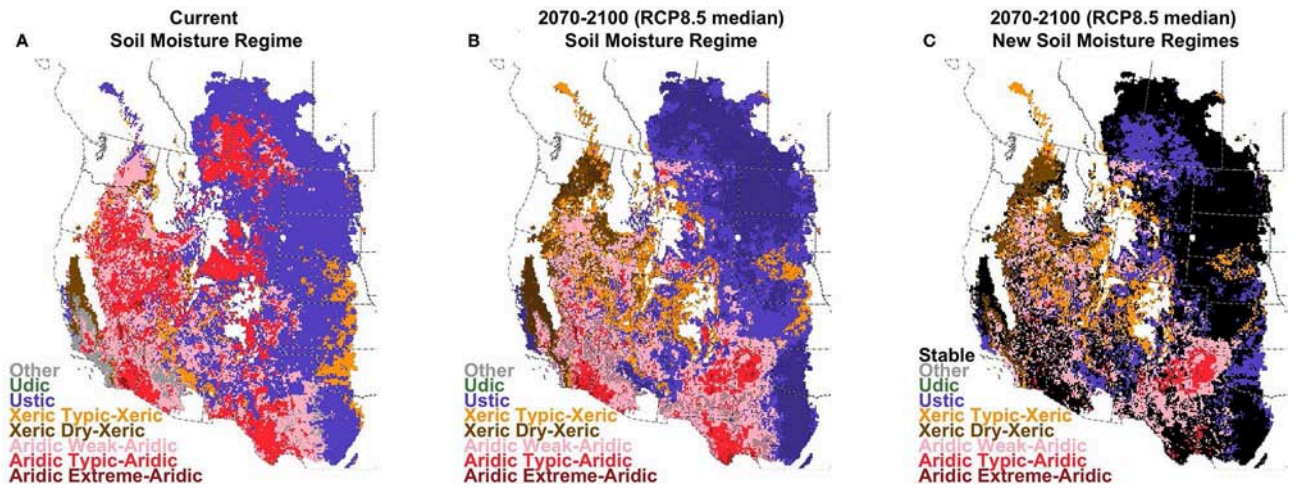

FIGURE 8 | Current **(A)**, future (**B**; 2070–2100; RCP8.5 median model), and change **(C)** in soil moisture regimes. Stippling indicates areas where >90% of climate models agree on the assignment of the regime under future conditions.

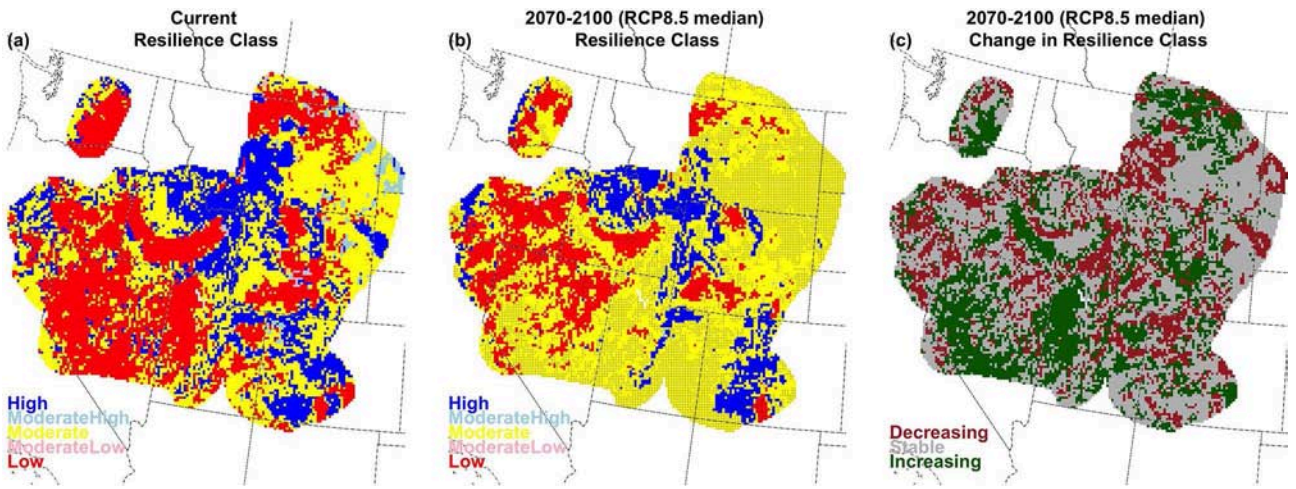

FIGURE 9 | Current **(a)**, future (**b**; 2070–2100; RCP8.5 median model), and change **(c)** for resilience in big sagebrush areas, characterized by greater sage-grouse management zones, which are outlined here.

moisture displays important variability in response to texture. Projected future increases in soil temperature, and resulting consequences for the distribution of soil temperature regimes, were very consistent across soil types (**Figures S3.1**, **S3.2**). Sandy loam soils had lower DRY_{PROP} than either the clay loam or silt loam soils, and generally lower than the site-specific soils (except where local soil texture is extremely coarse; **Figure S3.3**). Sandy loam soils also generally displayed higher wet soil days in the winter ($CWET_{WINTER}$; **Figure S3.4**) and slightly lower dry days in the summer $CDRY_{SUMMER}$; **Figure S3.5**) than the other textures. These differences mean that, compared to silt-loam or clay-loam soils, sandy loam soils support slightly less area with aridic soil moisture conditions and slightly greater area with ustic and xeric conditions although these differences decrease under future climate conditions when aridic soil moisture regimes are less common for all soil textures (**Figure S3.6**). Although the regional abundance of R&R categories are relatively similar among the soil types, the detailed geographic patterns of these categories do vary by soil type (**Figures S3.7**, **S3.8**).

DISCUSSION

Quantitative evaluation of climate vulnerability and ecological resilience to global change at broad spatial scales requires widely available information about relevant environmental conditions that influence how ecosystems respond to stressors like drought, invasive species, and disturbance (Chambers et al., 2019a). In dryland regions, soil temperature and moisture regimes are widely utilized as foundational

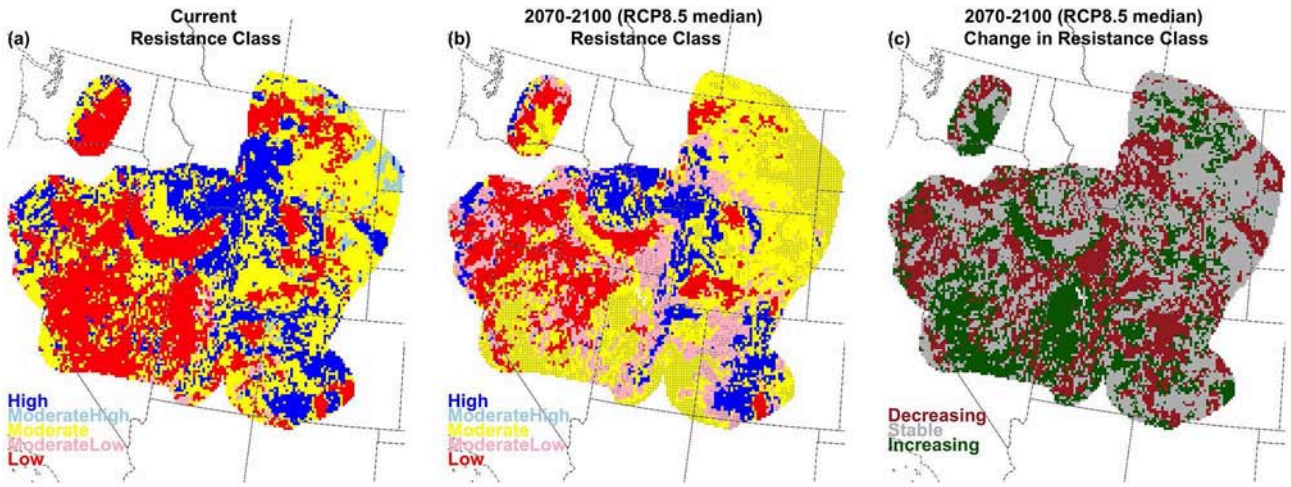

FIGURE 10 | Current **(a)**, future (**b**; 2070–2100; RCP8.5 median model), and change **(c)** for resistance in big sagebrush areas, characterized by greater sage-grouse management zones, which are outlined here.

indicators of resilience to disturbances, such as wildfire, and resistance to invasive plants, such as non-native annual grasses (Chambers et al., 2019b). By estimating how long-term climate trajectories will alter these regimes, our results provide insight into potential refinements that may help existing landscape-scale assessments of resilience and resistance better capture dryland ecological dynamics in a shifting climate.

Consistent Temperature Increases

Projections for substantial soil temperature increases in the twenty-first century are the most unambiguous and geographically consistent result from this analysis. Soil temperatures increase between historical and the 2020–2050 timeframe, and continue to increase substantially by 2070–2100, exemplifying the long-term divergence between historical and future climate conditions. More than 90% of the climate models concurred that air temperature and annual soil temperature will rise across the entire dryland domain and these increases are very consistent among soil types. Nearly the entire domain displayed similar consistent projections for increasing summer soil temperature. Soil temperatures are influenced by long-term effects of both air temperature and precipitation patterns, and these increases underscore the magnitude of change in energy balance expected. Higher soil temperatures may influence ecosystem carbon fluxes by promoting higher respiration rates that result in overall decreased ecosystem carbon stocks (Davidson and Janssens, 2006). This net release of carbon may alter the global carbon cycle, potentially increasing atmospheric carbon dioxide concentrations and providing a positive feedback to ongoing global warming (Bond-Lamberty et al., 2018). In addition, these rising temperatures highlight the growing risk for hot droughts in these already water limited ecosystems (Overpeck, 2013).

Geographic Variability in Moisture Projections

While projections for increasing temperature display relative geographic consistency, our results suggest substantial geographic variation in anticipated changes to soil moisture conditions. The largest divergence is between the central and northwest portion of our study region, where soil moisture availability appears likely to increase, and the southeastern portion, where soil moisture is expected to decline. The northwestern areas of our study region include the intermountain zone in the United States and much of the northern Great Plains, including southern Alberta and Saskatchewan. For broad areas within this area, several variables indicate increasing moisture availability that are robust across climate models, including decreases in the proportion of warm days with dry soil (**Figure S1.9**), decreases in overall days with soils that are entirely or partially dry (**Figures S1.11**, **S1.12**, respectively), and increases in days with entirely wet soil in the winter (**Figure S1.13**)

Ecosystems historically dominated by big sagebrush (*Artemisia tridentata*) are a major component of the areas with projections for increasing moisture availability. In recent years, big sagebrush ecosystems have become an important focus for policy makers and natural resource managers because of the widespread changes in vegetation structure and plant species composition (Knick et al., 2011) that impact the value of these systems as crucial wildlife habitat (Connelly et al., 2000; Crawford et al., 2004). Many of the moisture variables indicate increases in soil moisture availability in the future across areas with plant communities dominated by big sagebrush, implying that they may be able to persist under a changing climate if the plant communities can adapt their phenology in response to hotter, drier summer conditions accompanied by wetter, warmer spring and fall seasons (Palmquist et al., 2016a; Renwick et al., 2017). In particular, within regions established to

guide the management of the big sagebrush-dependent greater sage grouse (*Centrocercus urophasianus*), the abundance of aridic soil moisture regimes are expected to decline while the abundance of xeric regimes increase. It is important to note that the declining abundance of areas with aridic soil moisture regime within the big sagebrush region is driven by a decline in the proportion of warm soil days that also have dry soils (which is the criteria used to determine if a site qualifies for the aridic moisture regime designation). This metric of aridity may not be an optimal measure of the severity of ecological drought, as illustrated by the fact that most sites within the big sagebrush region are also expected to display increases in the number of hot days, and increases in the number of hot and dry days. In addition, the projections for modest increases in soil moisture in big sagebrush ecosystems by no means indicates that those systems are not imperiled by global change; interactions among wildfire and invasive annual grasses are major contributors driving historical big sagebrush decline (West, 2000; Knick et al., 2011; Balch et al., 2013), and loss of big sagebrush in response to these fire-invasive dynamics may continue in spite of stable or increasing moisture availability.

In contrast to the northwest and north-central regions, the southeastern and south-central portion of our study region displays uniform projections of declining moisture availability. These areas include the central and southern Great Plains and most of northern Arizona and New Mexico. Indicators of declining soil moisture availability that are robust across climate models for at least some of these areas include an increasing proportion of warm days that have dry soil (**Figure S1.9**), increasing dry soil days (**Figures S1.11**, **S1.12**), decreasing days with wet soil in the winter, and, for the central and southern Great Plains, decreasing days with wet soil in the summer (**Figure S1.14**). Previous studies have identified both the southwest and the central/southern Great Plains as areas with expected increases in aridity in the twenty-first century (Cayan et al., 2010; Seager and Vecchi, 2010; Cook et al., 2015), and our results about long-term declines in soil moisture underscore the potential consequences of this high exposure to climate change for resilience and resistance of these dryland ecosystems and the services that they provide (Bradford et al., 2017).

In addition to these broad regional patterns, the differences among soil types in soil moisture conditions, and future trajectories, suggest that edaphic conditions may play an increasingly important role in determining patterns of soil moisture. In particular, the sandy loam soils supported more favorable conditions for many of the soil moisture metrics, including lower proportion of warm days with dry soils (**Figure S3.3b**), more wet days in the winter (**Figure S3.4b**), and less dry days in the summer (**Figure S3.5b**). Many of these soil-driven differences are maintained or enhanced under future climate conditions.

Implications for Assessing Resilience and Resistance

The application of soil temperature and moisture regimes to define categories of ecological resilience to disturbance and resistance to invasive annual grasses has been most developed for big sagebrush ecosystems (Chambers et al., 2014b,c, 2019a,b; Williams and Friggens, 2017) where the framework has been used to prioritize conservation investments and land management strategies (Chambers et al., 2017a, 2019b; Crist et al., 2019). The approach used to define the current resilience and resistance categories involved identifying the dominant ecological types that currently exist in the sagebrush biome, determining their estimated soil temperature and moisture regimes based on mapped products from the National Cooperative Soil Survey, and then assigning resilience and resistance categories based on the available literature and expert knowledge (Chambers et al., 2014a, 2016, 2017b; Maestas et al., 2016). Our projections for the future of those regimes indicate two important considerations for long-term application of the framework using soil temperature and moisture regimes as the indicator of resilience and resistance.

First, the substantial increases in soil temperature, and the resulting expectations for shifting soil temperature regimes, imply geographic shifts in sagebrush ecological types and in ecological resilience and resistance categories across the landscape. Big sagebrush plant communities typically do not exist in areas with thermic soil temperature regimes and our results indicate that thermic soil temperature conditions will become more prevalent in the future, including in some areas currently occupied by big sagebrush. Because resilience to disturbance is assumed to decline with each transition to a warmer soil temperature regime (e.g., from cryic to frigid to mesic; Chambers et al., 2014c, 2016; Maestas et al., 2016), these rising temperatures, and associated shifts in soil temperature regimes in big sagebrush ecosystems may have dramatic impacts on future resilience and resistance of big sagebrush ecosystems. Specifically, changing from mesic to thermic soil temperature conditions may represent a shift from conditions that support big sagebrush plant communities to conditions that would be expected to support warmer and drier Cold Desert plant communities or even Mojave Desert plant communities in some areas (Rehfeldt et al., 2012). Also, these shifts may mean that these areas no longer have the climatic potential to support the dominant non-native invader, cheatgrass (*B. tectorum*), and that it may be replaced by red brome (*B. rubens*) or other non-native invasive plant species (Bradley et al., 2016).

Second, applying the expected shifts in soil temperature and moisture conditions using the current framework will estimate an increasing proportion of the big sagebrush region as intermediate R&R categories (**Appendix 2**). Currently, high or moderately high resilience or resistance in big sagebrush ecosystems is primarily associated with cryic or frigid temperature regimes (Chambers et al., 2014a,b, 2017b, 2019a), conditions projected to decrease in the future. In contrast, aridic soil moisture conditions are typically associated with low resilience and resistance in big sagebrush ecosystems. In the future, fewer areas will satisfy the criteria for aridic soil moisture regimes because aridic conditions are defined by the proportion of warm soil days that are also dry, and in most big sagebrush areas, warm days are increasing faster than warm-dry days. Although more areas would be classified as having moderate resilience and resistance

based on this criterion alone, the effects of this change on sagebrush ecosystems and their relative resilience and resistance are difficult to predict. Focused monitoring and research in sagebrush ecosystems can update understanding of relationships among climate, soil and vegetation, responses to stressors and disturbances, and vulnerability to climate and drought. Identifying and formalizing metrics of environmental conditions that represent ecologically meaningful variation can improve estimates of ecological resilience and resistance. Ecologically appropriate metrics can be based upon abiotic conditions like climate and soils, as well as biotic conditions assessed using monitoring data and emerging remote sensing technology (Jones et al., 2018).

Our results about the future distribution and abundance of areas categorized as having aridic soil moisture conditions highlight a limitation in utilizing the soil temperature and moisture regimes for assessing ecosystem resilience in the context of long-term directional change in climate conditions. In particular, relying on the proportion of warm days that also have dry soils to determine if a site has an aridic soil moisture regime suggests that the soil moisture regimes, as currently calculated, may struggle to represent the drought consequences of increases in both warm and dry days. As soil temperatures increase, the total number of warm days increases substantially, whereas the number of dry days often increases more slowly, reducing the proportion of warm days with dry soils. As a consequence, broad areas currently categorized as aridic soil moisture conditions will shift to other categories, despite the fact that many of them will have increases in the total number of days with dry soil (**Appendix 2**).

An important additional limitation of utilizing the current soil temperature and moisture regimes as indicators of ecological resilience and resistance is that the thresholds used to distinguish among the soil temperature and moisture regimes were not selected to represent ecologically meaningful thresholds, particularly for dryland environments. The regime definitions have been used for many decades, and our understanding of the environmental drivers of dryland vegetation dynamics has progressed substantially during that time (Vicente-Serrano et al., 2013). For big sagebrush ecosystems, which have been a major focus of previous resilience and resistance categorization frameworks, there are several recent studies identifying climatic and drought conditions that are important in shaping these systems (Coates et al., 2016; Palmquist et al., 2016b; Roundy et al., 2018).

One limitation to using soil temperature and moisture regimes as an indicator of resilience and resistance is that the regimes are defined by long-term conditions during "normal" years. These metrics can provide only limited insight into conditions during extreme events which have recognized impacts on ecosystems (Smith, 2011). Future refinements to R&R categories could include metrics that relate directly to the estimated severity of episodic, extreme drought, or drought and heat-wave conditions. Extreme events influence a wide variety of ecological processes, especially in dryland regions where precipitation and moisture availability are both important and highly variable (Gutschick Vincent and BassiriRad, 2003; Smith, 2011). For example, severe drought events can cause dryland plant mortality and decrease productivity in surviving individuals during subsequent years (Bigler et al., 2007; Bradford and Bell, 2017). At the other extreme, unusual wet conditions can interact with soil and stand characteristics to contribute to dryland plant mortality (Renne et al., 2019) as well as facilitate regeneration of perennial plants (Shriver et al., 2018), a notoriously episodic process (Schlaepfer et al., 2014; Petrie et al., 2016). Because the frequency and severity of extreme events can influence an ecosystem's composition, structure and susceptibility to biological invaders (Bradley et al., 2010; Reichstein et al., 2013; Ummenhofer and Meehl, 2017), incorporating metrics that represent ecologically relevant extreme drought conditions may improve assessments of resistance to invasion. Recognizing the role of extreme events may become even more crucial as climate change continues in coming decades, because the importance of extremes in shaping ecosystems may increase as extreme events become more frequent and intense (Stocker et al., 2013; Zhang et al., 2013).

Despite these limitations, soil temperature and moisture regimes have provided a practical indicator for contemporary assessment of resilience and resistance of North America's largest dryland ecosystem. The current R&R framework uses the available soil temperature and moisture regimes to represent geographic variability in environmental conditions and estimates how those regimes influence resilience to transformation due to wildfire, and invasive plant species. The differences that we observed in patterns of R&R categories among soil types suggest the existence of important, within-grid cell, soil-mediated variation in ecological resilience. This fine-grained variability may provide differential lagged responses to changing climate and/or climate refugia that may be important to resource managers. Our projections of future changes in the temperature and moisture variables that define these regimes indicate processes and areas with changes that are consistent among climate models, and suggest a focus for ecological monitoring that will increase our understanding of the changes in the resilience of these ecosystems in the twenty-first century.

These results suggest opportunities to enhance our quantification of geographic gradients in ecologically-relevant environmental conditions, currently represented by soil temperature, and moisture regimes, to sustain their long-term value as indicators of ecological resilience and risk-based management. One potential enhancement would be to assess the geographic distribution of temperature and moisture regimes using continuous time series of soil temperature and moisture data, either from a comprehensive network of observations or from process-based models as done here. These data, utilized in combination with existing soil survey information and other field measurements, could provide a useful tool for enhancing existing products produced by the National Cooperative Soil Survey and ensuring consistency across space and time. These data would allow managers to better forecast soil temperature and moisture regimes at regional scales with changing climate conditions. In addition, as long-term climate trajectories unfold, the links between

soil temperature and moisture conditions and ecological resilience and resistance need to be regularly re-evaluated to capture shifts in relationships between environmental conditions and ecological dynamics. Future assessments may include variables in addition to soil temperature and moisture regime classes that may be useful for understanding and representing important ecological thresholds in dryland ecosystems (Roundy et al., 2018).

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available in Bradford and Schlaepfer (2019), at https://doi.org/10.5066/P9PJFE82.

AUTHOR CONTRIBUTIONS

JB with help from DS and WL, designed the research. DS with input from JB, completed the simulations. JB with help from DS and input from all authors, analyzed results. JB drafted the manuscript. All authors contributed to editing the manuscript.

ACKNOWLEDGMENTS

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00358/full#supplementary-material

Appendix 1 | Detailed results for key variables. Layout for each variable includes maps under current conditions (top left), near-term and long-term under RCP 4.5 (top middle and top right, respectively) and RCP 8.5 (bottom middle and bottom right, respectively). Future maps illustrate the median climate model for each time period and RCP. Stippling in future maps indicates areas where >90% of climate models agree in either the direction of change (continuous variables) or the assignment of regime (soil temperature and moisture regimes). Horizonal boxplots of each variable, and the change in each variable are depicted in the bottom left, for current and future conditions. Boxplots of future conditions include the climate model representing the 10%, median (50%) and 90% of all models examined for each time period and RCP. Variables presented include.

Figure S1.1 | Mean annual temperature (MAT).

Figure S1.2 | Mean annual precipitation (MAP).

Figure S1.3 | Ratio of mean annual precipitation to mean annual potential evapotranspiration (MAP/PET).

Figure S1.4 | Mean annual soil temperature at 50 cm depth ($T50_{ANN}$).

Figure S1.5 | Mean summer soil temperature at 50 cm depth ($T50_{SUM}$).

Figure S1.6 | Soil temperature regime.

Figure S1.7 | Mean annual days with soil temperature at 50 cm > 5°C ($DAYS_{WARM}$).

Figure S1.8 | Mean annual days with all soil layers dry in the moisture control section when soil temperature at 50 cm > 5°C ($DAYS_{WARMDRY}$).

Figure S1.9 | Mean annual proportion of days when soil temperature at 50 cm > 5°C with all soil layers dry in the moisture control section (DRY_{PROP}).

Figure S1.10 | Mean annual maximum consecutive days with wet soil when soil temperature at 50 cm > 8°C ($CWET_8$).

Figure S1.11 | Mean annual number of days with all soil layers dry in the moisture control section (DRY_{ALL}).

Figure S1.12 | Mean annual number of days with any soil layer dry in the moisture control section (DRY_{ANY}).

Figure S1.13 | Mean annual number of consecutive days with all soil layers wet in the moisture control section during winter ($CWET_{WINTER}$).

Figure S1.14 | Mean annual number of consecutive days with all soil layers dry in the moisture control section during summer ($CDRY_{SUMMER}$).

Figure S1.15 | Soil moisture regime.

Appendix 2 | Results of regimes and resistance/resilience classification by sage-grouse management zone.

Figure S2.1 | Sage-grouse management zones. Zone 1: Great Plains; Zone 2: Wyoming Basins Zone 3: Southern Great Basin; Zone 4: Snake River Plain; Zone 5: Northern Great Basin; Zone 6: Columbia Basin; and Zone 7: Colorado Plateau.

Figure S2.2 | Projected proportions of each soil temperature regime for each greater sage grouse management zone.

Figure S2.3 | Projected proportions of each soil moisture regime for each greater sage grouse management zone.

Figure S2.4 | Lookup table for assigning resistance and resilience categories based on soil temperature and moisture, synthesized from previous studies.

Figure S2.5 | Layout for resistance within MZs.

Figure S2.6 | Layout for resilience within MZs.

Appendix 3 | Soil-specific results of key variables, soil temperature and moisture regimes, and resistance and resilience categories (for sage-grouse management zones). Results for continuous soil temperature and moisture metrics include current and future value for each variable under each soil type ("a" panels) and differences between site-specific soils (presented as the primary result in the manuscript) and each of the standard soil types. Results for categorical variables include only current and future estimates of the categories under each soil type and stippling indicates areas where >90% of climate models agree in the category assignment.

Figure S3.1 | (a,b) Mean annual soil temperature at 50 cm depth ($T50_{ANN}$).

Figure S3.2 | Soil temperature regime.

Figure S3.3 | (a,b) Mean annual proportion of days when soil temperature at 50 cm > 5°C with all soil layers dry in the moisture control section (DRY_{PROP}).

Figure S3.4 | (a,b) Mean annual number of consecutive days with all soil layers wet in the moisture control section during winter ($CWET_{WINTER}$).

Figure S3.5 | (a,b) Mean annual number of consecutive days with all soil layers dry in the moisture control section during summer ($CDRY_{SUMMER}$).

Figure S3.6 | Soil moisture regime.

Figure S3.7 | Resistance class.

Figure S3.8 | Resilience class.

Appendix 4 | Other information.

Figure S4.1 | Site-specific soil texture and moisture control section depth.

Figure S4.2 | Projected change in warm & dry days vs. projected change in warm days. Gray background points show all changes RCP 8.5, 2070–2100 vs. present. Colored isolines illustrate the distribution of changes for RCP4.5 2020–2050 vs. present (blue) and 2070–2100 vs. present (purple), and RCP8.5 2020–2050 vs. present (orange), and 2070–2100 vs. present (red).

Appendix 5 | Description of SOILWAT2.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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The Role of Social-Ecological Resilience in Coastal Zone Management: A Comparative Law Approach to Three Coastal Nations

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Around the globe, coastal communities are increasingly coping with changing environmental conditions as a result of climate change and ocean acidification, including sea level rise, more severe storms, and decreasing natural resources and ecosystem services. A natural adaptation response is to engineer the coast in a perilous and often doomed attempt to preserve the status quo. In the long term, however, most coastal nations will need to transition to approaches based on ecological resilience—that is, to coastal zone management that allows coastal communities to absorb and adapt to change rather than to resist it—and the law will be critical in facilitating this transition. Researchers are increasingly illuminating law's ability to promote social-ecological resilience to a changing world, but this scholarship—mostly focused on U.S. law—has not yet embraced its potential role in helping to create new international norms for social-ecological resilience. Through its comparison of coastal zone management in Australia, Finland, and the Netherlands, this article demonstrates that a comparative law approach offers a fruitful expansion of law-and-resilience research, both by extending this research to other countries and, more importantly, by allowing scholars to identify critical variables, or variable constellations associated with countries' decisions to adopt laws designed to promote social-ecological resilience and to identify mechanisms that allow for a smoother transition to this approach. For example, our comparison demonstrates, among other things, that countries can adopt coastal zone management techniques that integrate social-ecological resilience without fully abandoning more traditional engineering approaches to adapt to environmental change and its impacts.

Keywords: social-ecological resilience, coastal zone management, environmental change, law, environmental governance

INTRODUCTION

We face a world where climate change, ocean acidification, species extinction, and changing precipitation patterns are increasingly affecting human well-being. Despite these realities, law plays an important role in promoting human well-being despite these changing realities—that is, of promoting communities' resilience to environmental change. Coastal communities around the globe are already coping with significant changes from sea level rise, more frequent and increasingly severe coastal storms, and the progressive loss of coastal resources such as coral reefs and fisheries, as warming and acidifying waters interact with pollution and other stressors to severely degrade coastal ecosystems. Coastal zone management (CZM) provides a global focus for research on how law can effectively promote social-ecological resilience to the changes coastal communities are facing.

Over the past several decades, resilience theory and ecological resilience (Holling, 1973) have emerged as powerful tools for understanding the systems through which humans and nature interact, known as social-ecological systems (Berkes and Folke, 2000). Resilience theory describes how dynamic systems operating at a variety of spatial and temporal scales interact with each other, sometimes dampening change, sometimes accelerating it (Walker and Salt, 2006). For example, climate change reflects the fact that greenhouse gas emissions are destabilizing the climate system, a fairly large-scale system both spatially (it operates globally) and temporally (carbon dioxide remains in the atmosphere for centuries). The destabilized large-scale system, in turn, tends to accelerate changes in smaller-scale systems. Thus, warming temperatures both on land and in the ocean prompt species to migrate poleward or to higher elevations, disrupting food webs, and human food security (Craig, 2010).

Within resilience theory, and based on ecological resilience, "social-ecological resilience" refers to the ability of a social-ecological system to absorb change and disturbance without shifting to a new regime with a different set of processes and structures—i.e., without transforming into a new system state (Walker and Salt, 2006). Ecologists have documented repeatedly the ability of systems to transform—for example, prairies shifting from grassland to forest or eutrophication of freshwater lakes. Such transformations, and the threat of more transformations, have critical implications both for human well-being and for resource management (Brown and Williams, 2015).

As a corollary, resilience theory and the documented potential for social-ecological transformations have significant implications for law, governance, and policy (Garmestani and Allen, 2014; Humby, 2014; Benson and Craig, 2017). Law plays an essential role in shaping the discourse regarding social-ecological systems. For example, it helps to frame both how humans perceive their place within these systems and what risks are cognizable and actionable (Garmestani and Allen, 2014; Benson and Craig, 2017). Law can also promote the resilience of desirable social-ecological system states by, for example, mandating reduction of stressors like development and pollution, protecting essential habitat and ecosystem services, or limiting resource extraction to truly sustainable levels (Benson and Craig, 2017).

Over the last decade, research has increasingly focused on the implications of resilience theory for environmental law (Garmestani and Allen, 2014; Humby, 2014; McDonald et al., 2018; Garmestani et al., 2019). Nevertheless, so far, the scholarship exploring this relationship has been fairly limited and nation-centric. For example, previous research has tended to evaluate how well-specific existing laws in particular countries address the underlying features of ecological resilience and to offer recommendations for reducing the tension between social-ecological resilience and law. Moreover, most of this research and scholarship has been based on U.S. law (Ecology and Society Special Issue, 2013; Garmestani and Allen, 2014; Benson and Craig, 2017; Ecology Society Special Issue, 2018; Frohlich et al., 2018; but see McDonald et al., 2018; Wenta et al., 2018), providing little insight regarding the relationship between law and social-ecological resilience more generally. Finally, no scholars to our knowledge have actively engaged in a comparative law approach to assess what the differences and similarities among nations' legal approaches to similar management issues can teach us about the potential role of law in promoting social-ecological resilience for a changing world.

This article broadens the scope of research about the relationship between social-ecological resilience and the law. It pursues this goal by focusing on a policy issue common to most coastal nations: coastal zone management (CZM) in the face of environmental change. Specifically, this article compares CZM in Australia, Finland, and the Netherlands through the lens of resilience. CZM is a particularly apt subject for such a comparative law exploration because it has a long history of shared approaches to law and policy, facilitated by the widespread participation of coastal nations in the 1982 United Nations Convention on the Law of the Sea and other relevant international commitments such as the U.N. Convention on Biological Diversity, multiple treaties on marine pollution, and shared fisheries management. Advances in the science of ecosystem-based marine management (e.g., United Nations Environment Program (UNEP), 2011) and marine spatial planning (e.g., United Nations Educational, Scientific, and Cultural Organization (UNESCO), 2018) have similarly prompted significant international dialogue and guidance from the United Nations and its various agencies. Moreover, in the face of rising sea levels and increasingly severe natural hazards affecting coasts, many coastal nations are now introducing resilience-based approaches to coastal planning and management (Lloyd et al., 2013; Flood and Schechtman, 2014; Parsons and Thoms, 2017).

Thus, CZM provides a potentially fertile focus area for comparative law studies regarding the role of law in promoting social-ecological resilience: sea-level rise and other aspects of climate change (e.g., worsening or more frequent coastal storms) are already affecting coastal nations around the world; many of these nations engage in CZM and have been doing so for decades; and there are already international norms, best practices, and guidelines for CZM. All these harmonizing developments in the

global policy arena suggest that CZM will be a fertile starting point for comparative law research into resilience, because they are likely to reduce the idiosyncrasies between national legal frameworks, thus evading the most pressing challenge for all comparative legal research. We choose in this article to focus on three developed nations that have all engaged in CZM for some time but that have different government structures and that face different risks from climate change. The human population of Australia is concentrated along its coasts and deals with sea-level rise and other risks through a federalist system that divides regulatory authority between the National Government and the individual states and territories. Finland, like Australia, has a long coast, but it is less sparsely populated, with shared responsibilities in CZM between the central government, regional councils and municipalities. The Netherlands is a much smaller and more densely populated country, much of which is already below sea level, resulting in a long-term government focus on preventing inundation, with shared responsibilities between the central government and decentralized governments (provinces, municipalities, and regional water authorities).

As the next sections will explain in more detail, we posit as a normative goal that coastal nations should be seeking to transition to CZM based on an ecological resilience approach—that is, the use of techniques and processes to absorb and adapt to change rather than to resist it. Nevertheless, our assumption at the start of this study was that the three nations we studied would instead all exhibit a strong legal preference for management based on engineering resilience—that is, a reliance on coastal hardening and structures such as sea walls. While that assumption proved accurate in many respects, we also found that all three nations are beginning to experiment with the use of ecological resilience in CZM in response to sea-level rise, potentially reducing coastal adaptation problems several decades or a century from now and suggesting legal mechanisms that other nations could use to progressively transition to an ecological resilience approach. In other words, nations can take advantage of, in particular, sea level rise's longer time horizon to avoid disruptive and abrupt changes in their CZM laws and policies.

More importantly, this first foray into comparative legal analysis demonstrates the value of such studies in generating a more robust scholarship regarding the role of law in promoting social-ecological resilience to climate change and its impacts. This article therefore ends by suggesting further fruitful avenues of research in this field. For example, comparative analyses like the one we engage in here allow for assessments of whether particular local variables tend to promote engineering or ecological resilience approaches to CZM, as outlined in the next section, or whether the factors that induce a specific nation to adopt a particular CZM approach are idiosyncratic to each country. We hypothesize based on the results of this initial but limited foray into comparative analysis that both general patterns and important individual variations will emerge, and we encourage other researchers to join us in investigating this hypothesis.

GENERAL LEGAL APPROACHES TO RESILIENCE IN COASTAL ZONE MANAGEMENT: ENGINEERING VS. ECOLOGICAL RESILIENCE

The framing and goals of a country's CZM policies are critical for how well that nation addresses environmental change. If a nation's CZM laws seek to protect and preserve the coastal zone in its current configuration and functions, that strategy would reflect an engineering resilience approach (Holling, 1996; Walker and Salt, 2006). Many countries have indeed taken an engineering approach to coastal management, with a focus on increasing the capacity of their coastal zones to *resist* perturbance and change, such as sea level rise and increasing numbers of more severe storms, rather than to *adapt to* such changes. Engineering approaches to CZM tend to result in significant investments in coastal infrastructure, such as dikes, pumps, groins, seawalls, and other coastal armoring (Klein et al., 2001; Baughman and Pontee, 2016; Tetra Tech, 2019).

In contrast, other countries frame their CZM policies to improve the capacity of their coasts to absorb rather than to resist coastal change, reflecting an ecological resilience approach. Ecological resilience, as noted, refers to the capacity of a system to absorb change without transforming into a different state (Walker and Salt, 2006). Accordingly, acknowledging ecological resilience in legal policies necessarily acknowledges the potential for systems to transform. CZM strategies based on ecological resilience assume or acknowledge that the coastal social-ecological systems to which they apply could exist in different states, each with significantly different conditions and providing different ecosystem services (Holling, 1996; Lloyd et al., 2013; Flood and Schechtman, 2014). For example, coastal wetlands and marshes may offer storm protection and promote fisheries by providing extensive nurseries for fish but simultaneously increase the risks of mosquito-borne diseases for coastal populations. On the other hand, filled or "reclaimed" coastal wetlands lower this disease risk and may provide more opportunities for coastal recreation, but simultaneously reduce the capacity of local fish stocks to replenish themselves. Highly productive coral reefs that support tourism and fisheries transform into algae-covered rubble when exposed to warming and acidifying seawater and nutrient pollution.

Governments implementing an ecological resilience approach to CZM generally try to maintain or improve the capacity of coastal social-ecological systems both to adapt to environmental changes and to function at high levels of desirable productivity rather than striving to "freeze" current conditions in place. Such governments might restore and expand coastal wetlands, seagrass beds, mangroves, and other coastal ecosystems both to diffuse the impact of coastal storms and to maintain productive fisheries, or they might enact significant setback requirements and impose rolling easements on coastal properties that require removal of coastal infrastructure as sea levels rise, allowing productive coastal ecosystems to progressively migrate inland. Water law that mandates reductions in the pumping of coastal aquifers can stave off salt water intrusion (Craig, 2018; Delta Program, 2019),

while coastal cleanups, land use planning that limits long-term heavy infrastructure in the coastal zones, and improved building codes can reduce the coastal toxic load and hence the public health damage that storms can create (Craig, 2019). Finally, increased numbers of appropriately-located marine reserves can improve the resilience of marine ecosystems, marine biodiversity, and coastal fisheries to changing coastal conditions (Craig, 2012; Delta Program, 2019; Gilissen et al., 2019).

Whether a nation's CZM strategy is primarily underpinned by engineering resilience approaches or ecological resilience approaches has important ramifications for whether the coastal zones can continue to absorb and adapt to change (Allen et al., 2019). CZM framed (solely) as an engineering and infrastructure (engineering resilience) problem may well-result in the short-term stability of a nation's coast, but it tends to end with the loss of beaches and associated coastal ecosystems and increased armoring of coastal floodplains (e.g., Kittinger and Ayers, 2010). An engineering approach also risks catastrophic failure of the kind seen in New Orleans during and after Hurricane Katrina. In contrast, an ecological resilience approach to CZM may require coastal communities to migrate, perhaps more than once, in response to changing coastal processes. However, this approach is far more likely to ensure that functional and productive systems continue to exist into the future, even if those systems are transformed. These systems can in turn protect (e.g., storm surge dissipation) and support (e.g., through coastal fisheries) those shifting coastal communities (Kittinger and Ayers, 2010).

As a normative matter, therefore, laws in coastal nations should support the transition to CZM that takes an ecological resilience approach. We emphasize the need for legal *transition* because a nation's choice of CZM approach raises important trade-offs for law, policy, and politics that will change over time. These trade-offs can most basically be conceptualized as short-term social stability vs. long-term social-ecological productivity. How long the "short term" stable phase can last will often be critical to how governments and governance systems respond to coastal change. Moreover, the transition to ecological resilience approaches can legitimately take longer in some nations without substantially risking damage to either coastal communities or coastal ecosystems as a result of sea-level rise, other climate change impacts, or ocean acidification. Nevertheless, unless a coastal nation is so fortunately situated that it experiences no or very minor impacts from these drivers, eventually engineering approaches will cease to work and may even leave coastal communities worse off than if the infrastructure had never been built. Thus, the legal and management transition will (eventually) become necessary for most coastal countries.

DISTINGUISHING THE GENERALIZABLE FROM THE IDIOSYNCRATIC IN NATIONS' CZM LAWS AND POLICIES: THREE CASE STUDIES

Scientific projections regarding coastal social-ecological stability depend on a range of location-specific considerations, including the pace of local sea level rise and ocean acidification and the cumulative and synergistic risks to infrastructure or ecological assets. Such assessments are becoming more common and more accurate as the scientific community grows increasingly skilled at downscaling and localizing global climate change projections. However, given the variations among both social-ecological and cultural realities in the world's coastal nations, the social dimension of social-ecological resilience is also critical. For example, disaster resilience is one category of approaches to using law to promote social-ecological resilience in CZM. Disaster resilience has found traction in Australia, the United Kingdom, and the United States (Parsons and Thoms, 2017). Disaster resilience assessments rely primarily on *social* variables and conditions to judge a community's capacity to cope with disasters (Cutter et al., 2008). Nevertheless, disaster resilience approaches typically undervalue ecosystems and ecosystem dynamics, and thus CZM law and policy will need a broader approach to promoting social-ecological resilience (Chuang et al., 2018).

Given the number of variables involved, comparative law studies provide a valuable method for assessing not only whether and how coastal nations incorporate ecological resilience framing and techniques into their CZM, but also what variables emerge as critical to those decisions. Comparative studies allow researchers to question regulatory assumptions and to identify recurring dependencies, key variables, and common correlations. Comparative law studies can thus help to elucidate whether certain constellations of variables make it more likely that a nation will adopt ecological resilience approaches, which in turn can help to prompt both international law promotion of such techniques and wider knowledge sharing. Alternatively, such studies could demonstrate that the decision to pursue an ecological resilience approach depends so intimately on a nation's idiosyncratic social and cultural circumstances that the ecological resilience approach to CZM is unlikely to become an international or global legal norm and that nation-specific work is necessary.

At the start of this study, we hypothesized that the incorporation of ecological resilience into coastal nations' CZM is not entirely idiosyncratic. Our case studies support this hypothesis. And our analysis suggests that comparative law studies can increase the overall effectiveness of CZM law and policy in a changing world by paving the way for nations that share key variables to also share knowledge, experience, and techniques regarding ecological resilience approaches to CZM, easing the legal transition to that approach.

Australia: Emerging Efforts to Fit an Ecological Resilience Approach Into Coastal Infrastructure Protection

As an island continent, Australia has a vast and varied coastline (**Figure 1**). Over 85% of the nation's 24 million people live within 50 km of its 47,000-km coast, particularly concentrated along the east coast in major cities like Sydney, Melbourne, Brisbane and the Gold Coast, and larger regional coastal towns. The coastline is a mix of sandy beaches, rocky cliffs and mangrove or wetlands. Trade-offs between competing coastal uses in populated areas have typically favored intensive development, with associated

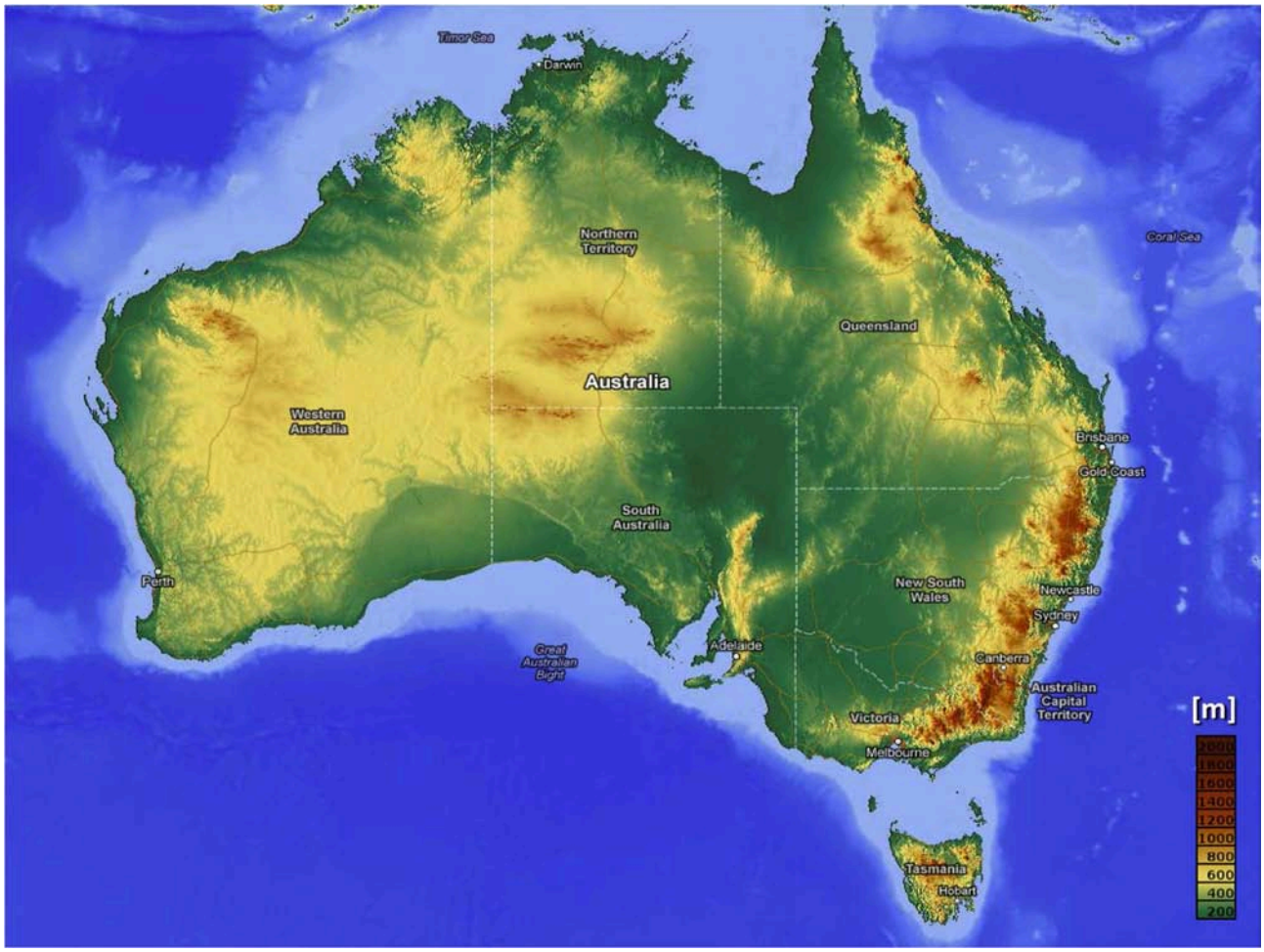

FIGURE 1 | Australia's topography. The darkest browns are 2,000 m above sea level. Source: https://i.imgur.com/6Ro7UFE.png.

degradation of coastal ecosystems (Clark and Johnston, 2016). There is extensive existing and high-value infrastructure either on the coastal margins or on low-lying coastal flood plains. This infrastructure includes over 810,000 km of roads, with a replacement value in excess of AUD$60 million. The value of railway lines at risk from coastal climate change impacts is estimated to be AUD$4.9–6.4 billion (DCCEE, 2011). The value of at-risk industrial and commercial infrastructure is over AUD$90 billion and residential infrastructure is over AUD$70 billion (DCCEE, 2011; Kirkpatrick, 2012).

The combination of coastal profiles and population density make Australia particularly vulnerable to the impacts of environmental change (Clark and Johnston, 2016). Beyond the obvious issues of coastal erosion and retreat, increases in the frequency and intensity of estuarine flooding of coastal floodplains is a major challenge (DCC, 2009; Clark and Johnston, 2016). Increased understanding of the likely impacts from sea level rise and extreme events has prompted a re-evaluation of coastal development patterns, at least in greenfield areas. However, the economic and cultural value of this existing legacy development constrains the potential for CZM approaches based on ecological resilience, because powerful political interests promote protection and armoring approaches over retreat.

Under Australia's federal system of government, the states have the legislative power over coastal management. There is no national CZM strategy or policy, and approaches to CZM are both fragmented and complex. Each coastal state and territory has a combination of laws and policies relating to coastal management, land use planning, conservation, fisheries, and catchment management, which all interact to influence coastal activities. Recent legal reforms have placed ecological resilience and climate change adaptation at the center of coastal management in Australia's two most populous states—New South Wales and Victoria[1,2], though the practical implications of these new objectives are yet to be felt.

While there are important legal differences across jurisdictions, the dominant model for dealing with new infrastructure and development involves mapping current and future coastal hazard areas over a range of timeframes and

[1]State of New South Wales, *Coastal Management Act 2016*.
[2]State of Victoria, *Coastal and Marine Act 2018*.

with differing assumptions about projected sea level rise, and then imposing limits on new development in areas identified as being at high risk. In all coastal states except New South Wales, the state government has adopted a sea level rise planning benchmark, which land use planning authorities are required to apply. The level varies across states but is generally set at about a 1.0 m rise above current sea levels by 2,100. New South Wales leaves the determination of what is an appropriate sea level rise planning benchmark to individual municipalities, which has resulted in significant legal variation depending on the property industry's influence and the local councilors' acceptance of climate change science within a specific municipality (McDonald, 2015).

States treat existing coastal development differently. Many coastal cities are already protected by seawalls, groins, and regular sand nourishment programs instituted after historical erosion events. A small number of regional coastal municipalities have introduced policies that require the removal of buildings affected by erosion in order to allow for coastal retreat (Foerster et al., 2015). In practice, however, the high value of beachfront properties has created intense political pressure in favor of protecting these exposed properties. At least one coastal authority has reversed its retreat policy, and governments mandate removal of structures only when sudden erosive events actually undercut houses so that they present an imminent threat to public safety (Macintosh et al., 2014; Foerster et al., 2015; McDonald, 2015). More often, media coverage of the homeowners' plight prompts emergency sandbagging and political promises of long-term protection. Together, these policies and reactions amount to a *de facto* engineering resilience approach. Indeed, in some cases, insurers have even overlooked policy exclusions for coastal hazards and paid out claims resulting from severe storm erosion, further entrenching an expectation that owners can repair or rebuild their properties in the same place.

Current engineering approaches also often squeeze coastal ecosystems. Coastal wetlands and heathlands have already experienced dramatic modification to allow for coastal development (McDonald and Foerster, 2016). Even when a particular location retains a ribbon of vegetation, the relevant laws and governments have made no allowance for natural inland migration in response to changed coastal conditions. In many cases, moreover, such migration would require removal of infrastructure on the landward side of such coastal reserves.

Of course, there are exceptions. For example, governments like the island state of Tasmania have acquired exposed properties when they come to market. This expanding government ownership creates greater flexibility when the time comes to implement a larger retreat strategy. Innovative approaches that align with a social-ecological resilience framing also include spatial planning designations of areas as "future coastal refugia" and limits on what development may occur on such sites (McDonald et al., 2018). So far, however, laws that promote an ecological resilience approach to CZM in Australia remain quite limited.

Finland: A Focus on Flood Protection and Resilience

Finland is located on the northeastern bank of the Baltic Sea and has an extensive indented shoreline of 46,000 km (Granö et al., 1999). The shoreline varies considerably, ranging from cliffs and moraine shores to gravel and sandy beaches (Granö et al., 1999). About 32% of the total length of the shoreline is dedicated to housing development and ∼1.5% to port and industrial development (Granö et al., 1999). The shoreline also hosts a series of nature conservation sites that are protected under European Union (EU) and domestic nature conservation law (Ministry of the Environment, 2006). Topographically, the coastal areas on the landward side of the UN Law of Sea Convention baseline are flat and prone to flooding (**Figure 2**). Roughly half of Finland's 5.5 million people live within 20 km of the sea shore (Ministry of the Environment, 2006).

Environmental change is driving sea level rise in the Baltic Sea. From a coastal management perspective, that sea level rise is partly offset by isostatic land uplift—i.e., the fact that the land is rising (Finnish Meteorological Institute, 2018). This mechanism is a legacy of the last ice age that ended roughly 11,500 years ago, when a thick glacier covered Finland (Finnish Meteorological Institute, 2018). Under the weight of this immense mass of ice, the ground condensed and sank. With the glacier largely gone, the ground is rising again; geologists expect the southern coast of Finland to rise about 40 cm and the northwestern coast about 90 cm over the next 100 years (Ministry of Agriculture and Forestry, 2005; Finnish Meteorological Institute, 2018). This natural mechanism will partly shield the social-ecological systems along the Finnish coasts from the adverse effects of rising sea levels—almost entirely along the northwestern coast but only partially along the southern coast. The capital city of Helsinki, located in southern Finland, concluded that, currently, the land uplift counters sea-level rise almost entirely, but also that sea level rise will become the more dominant phenomenon toward the end of the century (City of Helsinki, 2008).

Despite the shielding effect of land uplift, the Finnish coasts are expected to suffer from increased coastal flooding as a result of rising average temperatures, increased precipitation, snowmelt, and extreme weather events (Ministry of the Environment, 2006) (**Figure 2**). Especially strong winds combined with meteorological low-pressure areas and coastal currents can cause abrupt and significant sea-level rise and flooding, with harm to infrastructure, utilities, housing, industry and ecosystems (Ministry of Agriculture and Forestry, 2005).

Finland has adopted several national and municipal adaptation and coastal management strategies. These laws and policies seek, among other things, to minimize and adapt to the negative impacts of coastal flooding (e.g., Ministry of Agriculture and Forestry, 2005; Ministry of the Environment, 2006; City of Helsinki, 2008). These strategies emphasize the importance of planning, preparing for and adapting to coastal floods, and integrating adaptation strategies across sectors. The main mechanisms for preparing and adapting to coastal flooding are to: (1) steer housing and industrial development away from flood-prone areas; (2) build new and fortify existing flood

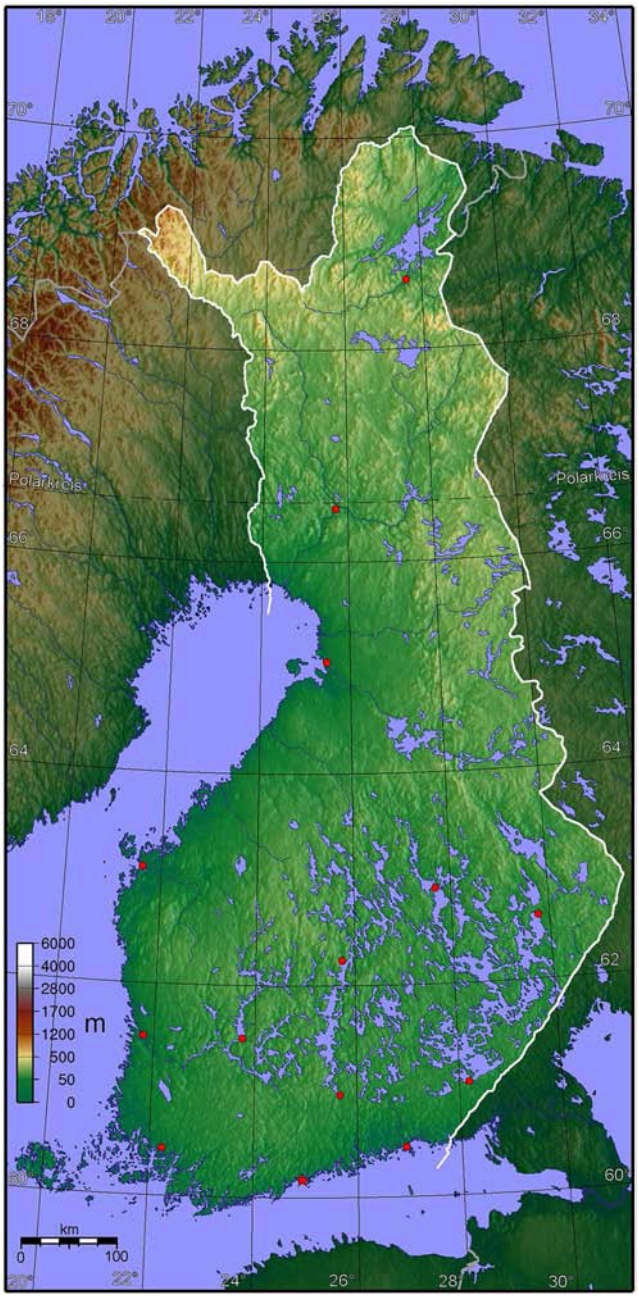

FIGURE 2 | Finland's topography. Most of the country of Finland rises no more than 50 m above sea level. Source: http://mapsof.net/uploads/static-maps/finland_topo_blank.jpg.

defense structures; (3) increase the capacity of municipal sewage systems to handle increased urban run-off; (4) increase the percentage of vegetation zones and decrease the percentage of paved urban areas to improve the soil's capacity to absorb water; and (5) use existing wetlands for flood management (Ministry of Agriculture and Forestry, 2005; Ministry of the Environment, 2006; City of Helsinki, 2008; Centre for Economic Development Transport the Environment in the Uudenmaa region, 2015). Thus, flood prevention policies in Finland already combine engineering resilience approaches—flood defense structures and sewage systems—with ecological resilience approaches, including development avoidance and the use of soil and wetlands to reduce flooding. Many of the ecological resilience approaches are, however, still at an experimental stage, and need to be upscaled in order to adapt to increasing coastal flooding toward the turn of the century.

Like Australia, CZM implementation in Finland is divided between several state and municipal actors and legal instruments. In flood protection, the two main instruments are land-use planning and flood risk management planning. As elsewhere, land-use planning's main objective is to steer the geographical location of housing, utilities, and industrial developments into preferred places. Land-use planning in Finland is divided between the state, regional, and municipal actors. These plans range in a hierarchical order from less to more specific: (1) national land-use objectives (national government); (2) regional plans (regional councils); (3) municipal master-plans; and (4) municipal detailed plans (Ministry of the Environment, 1999 p. 132). Regional and municipal plans are especially important in steering new housing and industrial development away from flood-prone areas (Ministry of Agriculture and Forestry, 2005; Ministry of the Environment, 2006).

Flood risk management planning is based on the EU Floods[3]. Such planning is science-based and incorporates: (1) an assessment of the likelihood of floods; (2) societal flood preparedness; and (3) societal recovery after a flood (Finnish Environment Institute, 2013). The main idea in flood management planning is that no new housing and industrial development should be allowed in flood-risk areas. These areas are mapped under the flood management planning regime, the results of which must be considered in planning and permitting new residential and industrial development. Flood management planning integrates the most up-to-date climate and flood models into land-use planning and other government and municipal actions. In the capital area of Helsinki, for instance, most flood-management measures planned and new building permits issued are based on flooding levels that occur, in statistical terms, every 250 years (Centre for Economic Development Transport the Environment in the Uudenmaa region, 2015). Translated into current mean water levels, this safety margin allows new infrastructure to cope with sea level rise of 0.87 m, or 34.25 inches (Centre for Economic Development Transport the Environment in the Uudenmaa region, 2015).

Nature conservation also plays a vital role in Finland's CZM. Traditionally, all nature conservation strategies relied on a static approach seeking to shield ecosystems from change (Aapala et al., 2017). This strategy is becoming increasingly problematic in light of ongoing environmental change, and new approaches are needed. Current research emphasizes the need for "climate smart conservation," which evaluates the impact of environmental change on protected species and areas and then adapts protective

[3] *Directive 2007/60/EC on the Assessment and Management of Flood Risks*. OJ L 288, 6.11.2007, 27–34.

measures accordingly (Aapala et al., 2017). This approach has yet to become mainstream in either EU/Finnish nature conservation in general or CZM specifically. Nevertheless, the identification of best practices for more ecologically resilient nature conservation policies is currently underway (Aapala et al., 2017).

In sum, Finland's adaptation strategies and coastal management have relied on the natural land uplift that has until recently compensated for all or most of sea level rise, as well as some of the negative impacts of coastal flooding. As this natural benefit becomes increasingly less effective, however, Finland is developing more active measures that span the engineering and ecological resilience spectrum to deal with environmental change. Engineering resilience is present in the state and municipal strategies and plans to build new and fortify existing coastal flood protection infrastructure, as well as in efforts to increase the capacity of municipal drainage systems to deal with increased precipitation and urban runoff. In addition, current nature conservation policies and laws are based on an engineering approach because they seek to shield protected areas and species from any adverse impacts from climate change.

Ecological resilience approaches are most visible in policies to reduce the percentage of urban paved areas and to promote nature-based solutions, such as using existing wetlands to help manage floods. Steering new development away from flood-prone areas can also be considered an ecological resilience approach because it allows the natural coastal environment to deal with and adapt to sea level rise and coastal flooding. However, this strategy is often not available in developed areas, because existing housing and industrial permits commonly enjoy legal finality and cannot be re-evaluated or modified in light of new scientific knowledge about sea level rise and flood risks. This remains one of the most pressing challenges for shifting existing infrastructure onto a more climate resilient path.

The Netherlands: Nascent Ecological Resilience Approaches in the Face of an Existential Threat

A delta region located in the northwest of continental Europe, 18% of the Netherlands' territory (41,526 km^2) is covered by water (Van de Ven, 2003). Over 35% of the country, including 65% of its population (of a total of 17,358,662) and invested capital (GNP of roughly $740 billion) is currently flood prone, with about one-third of these areas already situated below sea level (Van Rijswick and Havekes, 2012; also see **Figure 3**). As a result of a centuries-long struggle with water, a highly dedicated and technocratic flood risk governance structure developed in the Netherlands (Kaufmann et al., 2016), testifying to a deeply engrained, and prevailing cultural/political norm to prevent the hinterland from flooding while maximizing socioeconomic development and habitability of the land (Van Rijswick and Havekes, 2012). In practice, this norm requires the nearly constant drainage of over 3,000 polders and the maintenance of nearly 4,000 km of primary flood defense structures, including the coastal flood defense system.

Sea level rise will strain this system, but fundamental changes in law and policy are unlikely in the short term. Recent estimates indicate that sea level will rise 1.8–2.0 mm per year on average, resulting into a total of 25–80 cm by 2,085 (Royal Netherlands Meteorological Institute (KNMI), 2015). In contrast to Finland, moreover, land subsidence—resulting mostly from peat land compaction in the western parts of the country—is making the Netherlands' sea level rise problem even worse, although regional estimates differ considerably (Royal Netherlands Meteorological Institute (KNMI), 2015). The effects of climate change stress the current system and might eventually force toward more radical strategies such as large-scale relocations, but the Dutch flood defense strategy will continue to ground future flood risk governance in the Netherlands (Gilissen, 2015; Kaufmann et al., 2016; Delta Program, 2019).

The 523-km-long Dutch coastline stretches from the southwestern peninsulas (Scheldt estuary/Rhine-Meuse delta) to the Wadden Islands/Wadden Sea Region in the north and the Ems-Dollard estuary in the northeast (**Figure 3**). Although this coastline consists mainly of a nearly continuous stretch of sandy beaches and sand dunes, it also incorporates constructed flood defense infrastructure, such as the world-famous Delta Works (mostly in south-western delta but also including the Afsluitdijk) and industrial areas/sea ports, such as Rotterdam, Vlissingen, Den Helder, and Delfzijl. Coastal towns that are home to a flourishing tourism and recreational sector also dots the Dutch coast. The Dutch government has designated large parts of the coastal system as protected areas—Natura 2000 Areas and/or Ecological Main Corridors—under EU and domestic nature conservation law (Backes et al., 2017). Moreover, the Wadden Sea Region in the north of the country is one of the largest protected wetland areas in the world and has been designated as both a Natura 2000 Area and a UNCESCO World Heritage site.

As noted, the Dutch coastline plays an essential role in preventing the hinterland from flooding and, given its sandy nature, forms a particular domain within the Dutch flood risk governance structure (Van Rijswick and Havekes, 2012). Focusing on the sandy parts of the Dutch coastline, both flood defense and environmental protection are key components of Dutch CZM. Moreover, since the early 1990s, so-called "dynamic management" has been a key concept in Dutch CZM (Stronkhorst et al., 2018). The Dutch Technical Advisory Committee for Flood Defense defined "dynamic coastal zone management" as "managing the coast in such a way that natural processes, whether stimulated or not, can take place undisturbed as far as possible, as long as the safety of the inland area is ensured" (De Jong et al., 2014). The main objective of dynamic CZM is to prevent sand dune systems from eroding further and moving inland, thus maintaining a fixed coastline (CPD, 1990; see also https://www.rijkswaterstaat.nl/kaarten/kustlijnkaart.aspx). Under Article 2.7 of the Dutch Water Act of 2009, Rijkswaterstaat, the Dutch Central Government's Water Management Agency, achieves this stabilization where possible through flexible mechanisms to foster continued ecological integrity, including coastal ecosystem preservation, the maintenance of specific functions, and species protection based on EU/domestic nature conservation law (De Jong et al., 2014). Rijkswaterstaat's most common coastal management techniques is near-shore sand nourishment, a so-called "soft engineering"

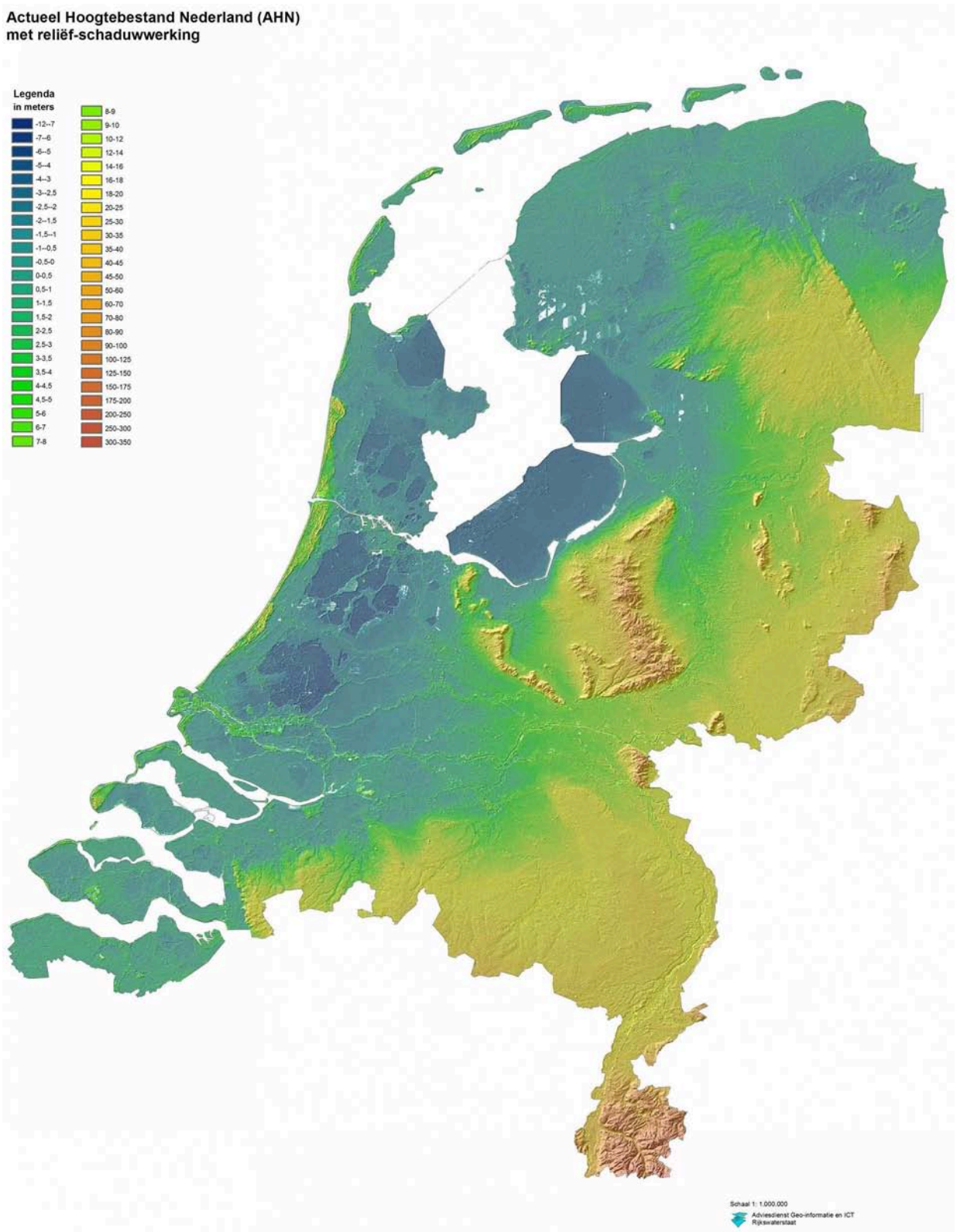

FIGURE 3 | The Netherlands' topography. The darkest blue areas are 7–12 m below sea level, while the deepest red areas reach 350 m above sea level. Gold areas are 25–40 m above sea level. Source: Netherlands Topographic 3D Map MakerEdChallenge 2 0 by mitrasmit, thingiverse.com.

approach, also dubbed a "Building with Nature" approach (Van Slobbe et al., 2013; De Vriend et al., 2015). Through this technique, large amounts of sand are pumped or transported to the shallow waters adjacent to the coast, allowing natural processes (mainly tides, waves, and wind) to gradually transport the sand landward, where it can elevate beaches, stabilize dunes, and, where needed, restore eroded sites and reverse related ecological degradation (Arens and Wiersma, 1994; De Ruig and Hillen, 1997; Van Dalfsen and Aarninkhof, 2009; Stive et al., 2013; De Jong et al., 2014). Dynamic CZM thus strategically aims to create a robust and resilient coastline and dune system that has the capacity to recover from erosion and related damage after storms and storm surges. Thus, the Netherlands pursues its overall engineering resilience goal through a generally effective and efficient strategy that blends engineering and ecological resilience approaches by spurring natural sand replenishment.

Nevertheless, overall, the Netherlands strives to keep its coastline and dune system stable and resistant to natural evolution, an inherently engineering resilience approach to CZM. Indeed, many policy documents use the term "veerkracht" (resilience) to refer to the coast's ability to bounce back to the status quo. In addition, this engineering resilience approach will not be ending any time soon: with a predicted sea level rise of 0.25–0.80 m by 2085 (Royal Netherlands Meteorological Institute (KNMI), 2015), the Dutch long-term (2,100) adaptation plan calls for intensified sand supplementation (Van Rijswick and Havekes, 2012; Delta Program, 2019), and the first pilot projects have already started (e.g., Project "Sand Motor"; De Schipper et al., 2016).

Moreover, hard engineering approaches remain important backstops to sand supplementation as sand supplementation does not always work to provide the legally required level of flood protection at some locations. These are the so-called "weak links" in the Dutch coastal defense system. At these locations, the relevant regional water management authorities have implemented additional or alternative measures to meet the legal security standards for "primary flood defense structures" (Article 2.4 of the Dutch Water Act 2009), such as building concrete constructions in dunes (Gilissen et al., 2010). In other words, where naturally driven processes fall short of meeting Dutch CZM goals, hard engineering remains a reliable solution, at least in the short to medium term.

Apart from flood protection, dynamic CZM through sand supplementation and other supportive measures (e.g., opening the Haringvliet sluices and flooding the Hedwigepolder) can be beneficial for environmental protection, contributing to the Dutch coast's and hinterland's ecological potential. Seven habitat types are present along the Dutch coast, and each is home to many protected and common species (http://natura2000.eea.europa.eu/). As noted, most of these areas are protected under EU and Dutch nature conservation law, which means that the Dutch government must preserve or improve their ecological values (Backes et al., 2017). However, Dutch (and EU) ecological policies have tended to emphasize ecological preservation and focus on saving specific species and ecological statuses, leaving little room for these systems to expand or transform. Thus, even though the Netherlands uses processes such as sand distribution to promote ecological function in large parts of its ecologically relevant coastal zones, the applied strategies still primarily embody an engineering resilience approach.

Comparative Analysis and Conclusions

Australia, Finland, and the Netherlands are developed nations, and they all have significant financial and infrastructure investments in their coastal zones. In addition, each nation has already significantly altered large swaths of its coastal ecosystems, losing considerable ecosystem function to development. As might be expected, the legal and policy framework of each country favors an engineering resilience approach to CZM that prioritizes the preservation of expensive and important coastal infrastructure, although each nation has also grafted on ecological preservation considerations pursuant to state (Australia), national, and EU (Finland and the Netherlands) law.

As such, the most important finding of this preliminary study is that, despite deep and pervasive historical legal and policy commitments to an engineering resilience approach to CZM, Australia, Finland, and the Netherlands each show signs of an emerging ecological resilience perspective. In Australia and Finland, both countries that still have relatively large amounts of space, this emergence primarily has taken the initial form of steering *new* development away from the coast, reducing future hardening of the coastal zone. The Netherlands, lacking this spatial luxury, has in some senses been far more creative in blending its engineering and ecological resilience perspectives.

Australian settlement consists of concentrated coastal development in urban areas. Law and policy in smaller coastal urban areas purport to favor a coastal retreat strategy, but in practice to date the overall emphasis continues to be on protecting and armoring shoreline infrastructure. This political reality constrains Australian CZM into an engineering resilience approach, at least in its highly urbanized areas. Property owners expect that they will be able to rebuild in the coastal zone after erosion or storm damage, which reflects an engineering resilience norm that seeks to have coastal communities bounce back to how they were before a disaster. With sea level rise and projections of more intense storm events, however, Australia will inevitably have to alter its approach to CZM, and some signs of this needed shift in CZM approach are appearing in New South Wales and Victorian state legislation and the approaches of smaller municipalities. Thus, at least some coastal managers in Australia appear to be adopting a perspective that acknowledges the dynamic nature of social-ecological systems, a nascent ecological resilience approach to CZM.

In Finland, CZM focuses on land use and flood risk planning that also has its roots in an engineering resilience approach. Government officials generally cannot re-evaluate existing development in coastal zones in light of new information (legal finality). Thus, current CZM in Finland leaves little room for adaptation to rising sea levels and flooding in developed areas; as a result, CZM instead must rely on coastal armoring to protect existing structures. Even so, as in Australia, there are signs that social-ecological resilience is seeping into Finland's CZM. Laws restrict new development in coastal zones, resulting in most new development occurring inland and freeing undeveloped

coastal areas to adapt to changing conditions. Finland is also experimenting with nature-based solutions, such as using existing wetlands for flood protection, and with increasing the amount of unpaved coastal urban areas, again strengthening the ability of coastal areas to adapt to changing conditions, such as increased flood risk.

The Netherlands literally has the least space of the three nations studies to absorb change and to adapt to changing conditions, as well as the strongest absolute social need to preserve coastal stability. Because ∼65% of the country's population already resides in flood prone areas, with a significant percentage of the country already below sea level, Dutch CZM is, unsurprisingly, characterized by engineered flood defenses of dikes and canals combined with large protected coastal areas designed to "freeze" the coastal system in a static state. This quintessentially engineering resilience approach to dealing with coastal system dynamics has been baked into Dutch culture and law for centuries.

Even in the Netherlands, however, ecological resilience approaches are emerging, albeit always subordinate to the overarching goal of coastal stability, an approach that some researchers have dubbed "Building with Nature" (Van Slobbe et al., 2013; De Vriend et al., 2015). Natural features such as sand dunes and beaches are legally recognized components of flood protection, meaning that Dutch CZM law and policy recognize the important ecosystem services that these features provide. Moreover, protecting and building up beaches and sand dunes is critical to the nation's overall CZM strategy. The "soft engineering" technique of sand distribution uses natural processes to ensure that these coastal features and their associated ecosystems and ecosystem services remain intact and well-functioning. In addition, recently there have been efforts to better protect and construct wetlands in order to supplement the system of dikes and pumps that keeps the country dry, hinting that the ecological resilience approach to flood protection is expanding in the Netherlands.

Beyond their individual trajectories, these three nations' approaches to CZM also suggest that the initial binary that this article proposed, contrasting an engineering resilience approach and an ecological resilience approach to CZM, in fact represents less of a dichotomy for coastal law and policy than a malleable ensemble of tools and strategies. In other words, the two approaches to CZM are not (entirely) mutually exclusive, and legal evolution can allow for the progressive emergence of an ecological resilience approach (see also Cheong et al., 2013). That full-scale legal revolution might not be necessary before a nation can implement the more adaptive approaches to CZM that are increasingly necessary in a changing world is an important finding in and of itself for legislatures and other policymakers (Garmestani et al., 2019).

However, the analysis of these three countries also suggests that legal and policy options for CZM will always be constrained by the physical realities of a particular coastal nation. The fact that sea-level rise is not a significant concern for large stretches of Finland's coast effectively gives Finland far more flexibility in its CZM approach than either Australia or the Netherlands will be able to tolerate. Essentially, climate change imposes less pressure on Finland to evolve its laws to an ecological resilience approach than it imposes on the Netherlands or, at the end of this extreme, disappearing Pacific island nations, simply because Finland's land mass is still responding to the retreat of ice-age glaciers.

IMPLICATIONS FOR FUTURE RESEARCH ON LAW AND SOCIAL-ECOLOGICAL RESILIENCE ALONG THE COAST

As we stated at the beginning of this article, the goal of this research project was not just to compare CZM approaches in Australia, Finland, and the Netherlands but, more importantly, to demonstrate the value of comparative law research in the study of law's role in promoting social-ecological resilience to changing environmental conditions. As limited in scope as this study is, our comparative analysis of these three countries already suggests several fruitful focal points for future research. For example, the realization that all three countries—admittedly, to different degrees—already deploy ecological resilience strategies and techniques within an overall CZM legal framework that privileges engineering resilience raises several important questions regarding the extent to which nations can and do blend these two approaches and whether blending evolves eventually into an ecological resilience-based approach to CZM. Research assembling a variety of case studies and documenting exactly how coastal law and policy are evolving in a variety of nations could thus provide important contributions to global CZM in the Anthropocene.

The realization that physical realities remain important factors in shaping a particular nation's CZM law and policy also suggests productive avenues for interdisciplinary research. Specifically, our initial three case studies suggest that the disciplines of legal geography and historical geography have important roles to play in investigating the intersection of resilience theory and CZM and in formulating effective future CZM law for individual nations.

More generally, a proposition to be tested in future research is whether coastal nations typically begin with an engineering resilience approach to CZM (and, indeed, to their environmental laws more broadly). Our three case studies are insufficient to discern, for example, whether this approach is globally typical, or is found mostly in European-derived government systems, or is found mostly in developed nations, or even is idiosyncratic to the three countries we happened to study (plus the United States). We also have not focused on whether the hard engineering approaches pre-dated CZM law and policy (i.e., law and policy reflect a reality that already existed) or occurred outside the law (i.e., CZM *practice* contradicts CZM *law*). If it turns out that countries with significantly different legal traditions and histories (e.g., minimal influence from European colonialism), or with significantly different economic statuses, than the three countries studied here typically employ an ecological resilience approach to CZM, further questions for research would emerge, such as: what factors prompt a coastal nation to adopt an ecological resilience approach to CZM from the beginning? How influential are factors such as a lack of intense coastal settlement and development, the cultural/religious importance of coastal

ecosystems, or deeply engrained social norms against building permanent infrastructure along the coast? Can these factors be generalized, or is each coastal nation in important senses unique?

A final consideration worthy of more comparative investigation is the fact that legal systems have different capacities to innovate within their CZM strategies based on factors such as enforcement mechanisms, flexibility in law, the rate of statutory change, and the role of litigation. For example, some legal systems already embrace doctrines that can be harnessed to promote the adaptation and evolution of CZM. In common-law systems derived from England and British colonialism (including the United States, Canada, Australia, New Zealand, and South Africa, plus extensive influence on various African and South American nations), concepts of public and private nuisance, trespass, negligence and strict liability, and in some, public trust, provide mechanisms for evolving natural resources law and policy (Rechtschaffen and Antolini, 2007). As one example, the States of Oregon, California, and Hawai'i in the United States have used the public trust doctrine to require holistic protection of aquatic ecosystems (Craig, 2010; Boisjolie et al., 2017). How do these different capacities affect the CZM approaches that nations take, or the evolution of those approaches in the face of environmental change?

This example also highlights the potential importance of subnational governance, a factor present to some degree in all three countries studies here. Those local, regional and state levels often have greater capacity to innovate because they can provide greater capacity for stakeholder engagement and an appropriate scale for experimental management approaches (Charnley et al., 2018). Nevertheless, super-national law can also be important in spurring innovation. Thus, as two examples, parties to the United Nations Convention on Biological Diversity and EU member nations are subject to ecological obligations that are supposed to influence, and in some cases can supersede, national proclivities toward a purely engineering resilience CZM approach, as is evident in both the Finland and Netherlands case studies here. Future research might well-investigate how governance pluralism, as is prominent in the United States, and hierarchical governance influence the ability of CZM law and policy to adapt to a changing world.

Clearly, different legal framings of resilience in the coastal zone have important implications for future coastal social-ecological resilience in the face of accelerating environmental change (Clarvis et al., 2013). The limited comparison presented here suggests that much fruitful work remains to be done through comparative law approaches to CZM. Specifically, our initial foray into this kind of approach strongly suggests that more extensive interdisciplinary and comparative research could provide coastal nations with numerous policy tools and legal mechanisms for transitioning to ecological resilience techniques for and approaches to CZM that will better promote continued (if transformed) productivity and social-ecological resilience in the face of sea-level rise, worsening coastal storms, warming seas, and ocean acidification.

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Spatial Imaging and Screening for Regime Shifts

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Screening is a strategy for detecting undesirable change prior to manifestation of symptoms or adverse effects. Although the well-recognized utility of screening makes it commonplace in medicine, it has yet to be implemented in ecosystem management. Ecosystem management is in an era of diagnosis and treatment of undesirable change, and as a result, remains more reactive than proactive and unable to effectively deal with today's plethora of non-stationary conditions. In this paper, we introduce spatial imaging-based screening to ecology. We link advancements in spatial resilience theory, data, and technological and computational capabilities and power to detect regime shifts (i.e., vegetation state transitions) that are known to be detrimental to human well-being and ecosystem service delivery. With a state-of-the-art landcover dataset and freely available, cloud-based, geospatial computing platform, we screen for spatial signals of the three most iconic vegetation transitions studied in western USA rangelands: (1) erosion and desertification; (2) woody encroachment; and (3) annual exotic grass invasion. For a series of locations that differ in ecological complexity and geographic extent, we answer the following questions: (1) Which regime shift is expected or of greatest concern? (2) Can we detect a signal associated with the expected regime shift? (3) If detected, is the signal transient or persistent over time? (4) If detected and persistent, is the transition signal stationary or non-stationary over time? (5) What other signals do we detect? Our approach reveals a powerful and flexible methodology, whereby professionals can use spatial imaging to verify the occurrence of alternative vegetation regimes, image the spatial boundaries separating regimes, track the magnitude and direction of regime shift signals, differentiate persistent and stationary transition signals that warrant continued screening from more concerning persistent and non-stationary transition signals, and leverage disciplinary strength and resources for more targeted diagnostic testing (e.g., inventory and monitoring) and treatment (e.g., management) of regime shifts. While the rapid screening approach used here can continue to be implemented and refined for rangelands, it has broader implications and can be adapted to other ecological systems to revolutionize the information space needed to better manage critical transitions in nature.

Keywords: diagnosis, early warning indicator, Google Earth Engine, proactive management, rangeland analysis platform, resilience, spatial resilience, treatment

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INTRODUCTION

Screening is widely applied to the early detection of undesirable change. Pioneering approaches to screening in medicine made it possible to detect diseases before consequences to health were realized by the individual or confirmed through practitioner diagnosis (Morabia and Zhang, 2004). The use of spatial medical imaging in early screening for a variety of diseases is now commonplace. It is important to differentiate between screening, which indicates the potential presence of a disease, ideally before the emergence of signs and/or symptoms, and diagnostic testing, which confirms the presence of a disease following the emergence of characteristics signs and/or symptoms or screening-based detection (Gilbert et al., 2001). Screening generates information that can be used to proactively diagnose and treat a disease, and thereby, avoid or mitigate its detrimental effects (Morris, 1994; Saunders et al., 2001).

Despite its clear utility in medicine, screening for undesirable ecological change (i.e., regime shifts; state transitions) has yet to be implemented in ecosystem management. Ecosystem management to date has largely focused on diagnosing (e.g., monitoring and inventorying) and treating (e.g., managing) regime shifts (**Figure 1**). It is not surprising then that ecosystem management as a whole has remained more reactive than proactive in an era of global change, uncertainty, and surprise. Even though ecology has long sought objective early warning indicators of regime shifts, in the language of medicine, most applications of early warning indicators are diagnostic, in that they are predicated on the detection of the signs and/or symptoms of change that has already begun to occur (Biggs et al., 2009; Dakos et al., 2015). Furthermore, many early warning indicators of ecological regime shifts require extensive data and *a priori* understanding of focal systems and/or the disturbances they experience (Gsell et al., 2016). This means that such applications may be incapable of objectively representing the risk of undesirable regime shifts prior to the manifestation of their symptoms, which limits preventative management efforts and leaves professionals reliant upon reactive strategies that lag behind transition signals.

The study of regime shifts in ecology is rooted in resilience thinking (Folke et al., 2010), where resilience is defined as the capacity of a system to absorb disturbance without transitioning to an alternative regime, whether the present or alternative regime is desirable or undesirable from a human perspective. Beyond its utility as a metaphor, the quantification of resilience has long been heralded for its potential to enhance the ability of management to prevent undesirable regime shifts; however, resilience quantification has proven notoriously elusive (Angeler and Allen, 2016). Among the major advances toward resilience quantification and operationalization in ecological management is Carpenter et al.'s (2001) recommendation to consider the "resilience of what to what" at the outset of any resilience-based assessment. In other words, identifying the focal system and disturbance(s) affecting it is fundamental for managing for resilience and avoiding undesirable regime shifts.

The "resilience of what to what" has factored into theoretical and quantitative advances in spatial resilience—an extension of resilience that can be defined simply as the contribution of spatial attributes to feedbacks that generate resilience (Allen et al., 2016). This includes, but is not limited to, the spatial arrangement of and interactions among internal system components, spatial variation in internal system phases (e.g., successional stages), and the system's spatial context (Cumming, 2011a,b). When disturbances exceed system resilience, regime shifts occur with spatial-temporal order (Sundstrom et al., 2017; Roberts et al., 2019). Through the lens of landscape ecology, one example of a spatial regime shift playing out over time is the spread of an initially rare invasive species patch through an initially abundant background landcover matrix. With some degree of spatial-temporal order, propagation of the invasive species fragments and reduces cover of the background matrix until the invasive species is so abundant and connected that it becomes the new background matrix, with the former matrix persisting only in isolated patches (Zurlini et al., 2014). When framed in succession theory, regime shifts may occur when alteration of historical disturbance regimes pushes systems into earlier or later successional stages. For example, increased fire frequency and severity may shift forests to woodlands and woodlands to grasslands, just as decreased fire frequency and severity may cause shifts in the opposite direction (Twidwell et al., 2013a; Fuhlendorf et al., 2017). There is certainly promise in enhancing understanding of systems and the disturbances that affect them, as well as in examining the spatial attributes of resilience and regime shifts from the perspective of different ecological subdisciplines; however, in returning to the language of medicine, these advances and explorations are more closely aligned with diagnosis than screening.

The development of approaches for screening for environmental change could contribute to improved decision-making in and effectiveness of ecological management. Undesirable regime shifts in ecological systems are often hysteretic (Scheffer et al., 2001), meaning that restoration is less feasible and more costly than if actions are put in place to avoid them from occurring in the first place (Holling and Meffe, 1996). Screening could be used to identify core areas of desirable regimes not yet experiencing regime shifts, which may be prioritized for preventative management that builds resilience of desirable regimes (Chapin et al., 2010). In the same way, areas in which screening indicates regime shift imminence may be prioritized for intensive management aimed at halting or reversing the regime shift. Finally, areas in which screening indicates that regime shifts have already occurred—particularly at large scales—or areas in which it is infeasible to halt regime shift advances, may explore avenues for transformation in law, policy, and governance to better deal the realities of the new regime (Chaffin et al., 2016; Garmestani et al., 2019).

Instead of replacing diagnostic approaches to regime shift detection, screening complements them and maximizes their utility. The absence of screening in ecosystem management up to this point in time is at least partly the result of data and computation limitations (Guttal and Jayaprakash, 2009); however, advances in technology and monitoring continue to make more accurate data available at greater

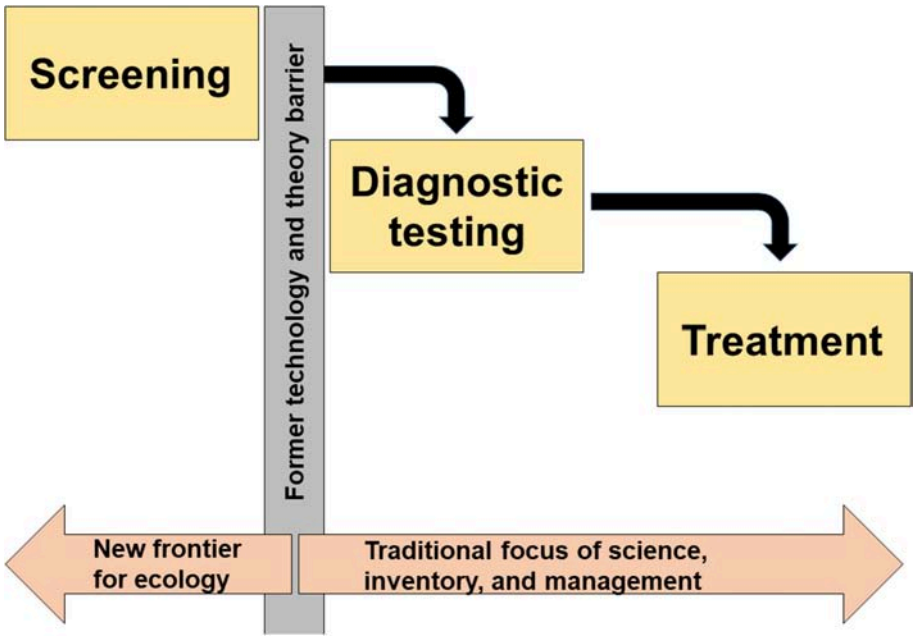

FIGURE 1 | In medicine, screening is used for early disease detection, prior to the emergence of disease signs and/or symptoms. Technological and theoretical barriers have prevented the implementation of screening methods in ecology, so the discipline has been largely reactive and incapable of dealing with large-scale undesirable changes that affect human well-being. Now, critical theory–data–technology linkages enable imaging and screening for ecological regime shifts.

spatial and temporal resolutions (i.e., grains) and extents (i.e., areas) (Pimm et al., 2015; Jones et al., 2018; Xie et al., 2019), and advances in geospatial cloud-computing enable efficient analysis of such data (Yang et al., 2011). At the same time, metrics are being developed in resilience science to quantify spatial contexts and signals that correspond with changes in ecological resilience, the collapse of ecological regimes, and their displacement by novel ecosystem states (Cline et al., 2014; Kéfi et al., 2014; Allen et al., 2016; Roberts et al., 2018a). Now, for the first time, critical components of theory, data, and technology are converging in linkages that make it plausible to screen for and image ecological regime shifts.

In this study, we introduce the practice of screening for the early detection of undesirable regime shifts in ecological systems, using rangeland systems of the Western United States as test cases. Rangelands are idealized systems for studying regime shifts, as different rangeland vegetation regimes (i.e., alternative stable states) are more-or-less desirable for certain suites of ecosystem services and are therefore the basis of ecosystem management (Westoby et al., 1989). Although not completely irreversible, undesirable regime shifts present considerable restoration challenges (Twidwell et al., 2013b), making it advisable to avoid shifts in the first place and to consider how screening might help do so. With a spatial informatics approach that links resilience theory with a state-of-the-art landcover dataset and a powerful cloud-computing platform, we screened for the following set of iconic rangeland vegetation transitions in landscapes of the western United States: (1) erosion and desertification; (2) woody plant encroachment; and (3) exotic annual grass invasion. In adherence to the First Law of Geography (Tobler, 1970), these regime shifts tend to manifest as spatially contagious processes, meaning that the likelihood that a location will experience a regime shift increases with geographic proximity to other locations that have experienced the shift. Simply put, spatial context is a critical determinant of a location's spatial resilience, and conversely, its spatial vulnerability to change.

During screening, we answer five questions: (1) Which regime shift is expected or of greatest concern? (2) Can we detect a signal associated with the expected regime shift? (3) If detected, is the signal transient or persistent over time? (4) If detected and persistent, is the transition signal stationary or non-stationary (i.e., moving) over time? (5) What other signals do we detect while screening? We then discuss the potential of our approach to detect vegetation transition signals and to characterize them according to their degrees of persistence and non-stationarity with little-to-no *a priori* understanding of focal system state, feedbacks, disturbances, or alternative stable states, and thereby, to contribute to more preventative and efficient management of rangelands and other ecological systems.

MATERIALS AND METHODS

Data, Metric, and Analytical Platform

We used a state-of-the-art rangeland landcover raster dataset and a powerful, freely-accessible, cloud-based, geospatial computing platform to rapidly screen for spatial regime shift (i.e., vegetation transition) signals in five rangeland-dominated landscapes of the western United States from 2000 to 2017. The landcover dataset contains yearly, 30 m resolution, continuous percent cover estimates for the following four plant functional groups and three abiotic landcover components (hereafter referred

to collectively as functional groups) in western United States rangelands from 1984 to2018: annual forbs and grasses, bare ground, litter, perennial forbs and grasses, rocks, shrubs, and trees (Jones et al., 2018), with rangelands delineated according to Reeves and Mitchell (2011). We used spatial covariance between functional group combinations as a screening metric. In rangelands, bare ground is representative of a state transition to an unvegetated state; however, litter has no basis as an alternative state and rock is stationary over the scale of our analysis. Therefore, neither percent litter nor percent rock were used for screening in this study, which reduced the number of contrasting functional groups to 5, and the number of unique pairwise functional group combinations to 10.

Our approach to regime shift screening emerges from resilience theory, which posits that a system exists in one, not multiple, regimes (i.e., stability domains; basins of attraction) at a time (Holling, 1973; Folke et al., 2010) and that transitions from one ecological regime to another exhibit spatial order at one or more scales of organization (Allen et al., 2016; Roberts et al., 2019). Given that alternative ecological regimes cannot occupy the same space over time, the simultaneous existence of multiple alternative regimes means that every regime is neighbored in space by an alternative regime(s)—each with its own reinforcing feedbacks and structures.

As a screening metric, we used a moving window algorithm to calculate spatial covariance between rangeland functional groups, where strong negative spatial covariance provides a geographic transition signal of regime boundaries that can be tracked through time. More generally, covariance is useful for highlighting boundaries and other correlations in data that averaging-based methods tend to smooth over (Frasinski et al., 1989; van der Heijden, 1995; Ando, 2000), and for decades, has been utilized to quantify spatial and temporal dynamics of ecological systems (Kershaw, 1961; Goodall, 1965; Noy-Meir and Anderson, 1971; Greig-Smith, 1983; Dale and Blundon, 1991; Wagner, 2003; Houlahan et al., 2018). Our selection of spatial covariance as a screening metric builds on the efforts of Pielou (1961), Goodall (1965), and other pioneers of methods for quantifying the spatial arrangement of ecological entities in relation to one-another. Functional groups that do not coexist should exhibit negative spatial covariance at their boundaries because of spatial irregularities (i.e., asymmetries, Norberg and Cumming, 2008) in their relational organization (i.e., tendency to separate from one another in space). In addition to quantifying the spatial arrangement of functional groups in relation to one another, spatial covariance is multivariate, and multivariate metrics tend to outperform univariate metrics in the detection of regime shifts in complex systems (Spanbauer et al., 2014; Roberts et al., 2018a). When computed in a moving window algorithm, spatial covariance also incorporates spatial context—an important external element of spatial resilience (Zurlini et al., 2006, 2014; Cumming, 2011a,b; Allen et al., 2016). Therefore, spatial covariance acts as an edge-detection technique, and importantly, one closely aligned with spatial resilience theory.

In the computation of spatial covariance, the more two entities are negatively associated with one another in space (i.e., one increases while the other decreases in a given area), the more strongly negative is their spatial covariance, whereas the more two entities are positively associated with one another in space (i.e., they increase or decrease together over the given neighborhood), the more strongly positive is their spatial covariance (Wagner, 2003). Spatial covariance of 0 means that no spatial relationship exists between two entities. In other words, spatial covariance provides a measure of the degree of coexistence between two entities. In the case of functional groups, more strongly negative spatial covariance provides a signal that emerges from the inability of two functional groups to coexist in a given space. For example, in **Figure 2**, strong negative spatial covariance mirrors the visual boundary between adjacent perennial grassland and tree regimes. With movement away from the boundary into either the core of grassland or forest regimes, perennial–tree spatial covariance increases from $<$-200 toward 0. The lack of trees within the core of the grassland regime results in the absence of a spatial relationship between grasses and trees in that area, just as the lack of grass within the core of the forest regime results in the absence of a spatial relationship between grasses and trees in that area.

To rapidly compute spatial covariance between pairwise functional group combinations at relatively high spatial resolutions and over relatively broad geographic extents, we used Google Earth Engine—a powerful, freely-available, cloud-based geospatial computing platform (Gorelick et al., 2017). Within Google Earth Engine, we applied the covariance reducer function (Pébay, 2008) in a moving window (i.e., neighborhood) analysis to compute spatial covariance over four geographic neighborhood sizes: 3 by 3 pixels, 9 by 9 pixels, 27 by 27 pixels, and 113 by 113 pixels. In the moving window analysis, all kernels were weighted uniformly with values of 1 (i.e., no distance decay within neighborhoods). Analyses were conducted at a spatial grain of 30 m for the 3 by 3 pixel (0.81 hectares), 9 by 9 pixel (7.29 hectares), and 27 by 27 pixel (65.61 hectares) neighborhoods, and at a spatial grain of 60 m for the 113 by 113 pixel (4,596.84 hectares) neighborhood. Larger neighborhoods incorporate more spatial context into map pixel spatial covariance outputs. For each map pixel in each year, the raw output of Google Earth Engine's covariance function is a spatial variance–covariance matrix, in which matrix diagonals are spatial variance values (i.e., the spatial associations of functional groups with themselves) and the top and bottom matrix triangles are spatial covariance values (i.e., the spatial associations of functional groups with one another). Because the top and bottom spatial variance–covariance matrix triangles contain identical values, we extracted and mapped values from the top triangle of each pixel's matrix in five focal landscapes between 2000 and 2017. We exported spatial covariance maps of all 10 functional group combinations in all years as raster images in GeoTIFF format for processing and visualization in ArcMap (Esri, 2016) and R (R Core Team, 2018), with the lattice (Sarkar, 2008), latticeExtra (Sarkar and Andrews, 2016), sp (Bivand et al., 2013), raster (Hijmans, 2018), RColorBrewer (Neuwirth, 2014), rasterVis (Lamigueiro and Hijmans, 2018), rgdal (Bivand et al., 2018), and stringr (Wickham, 2018) packages for R.

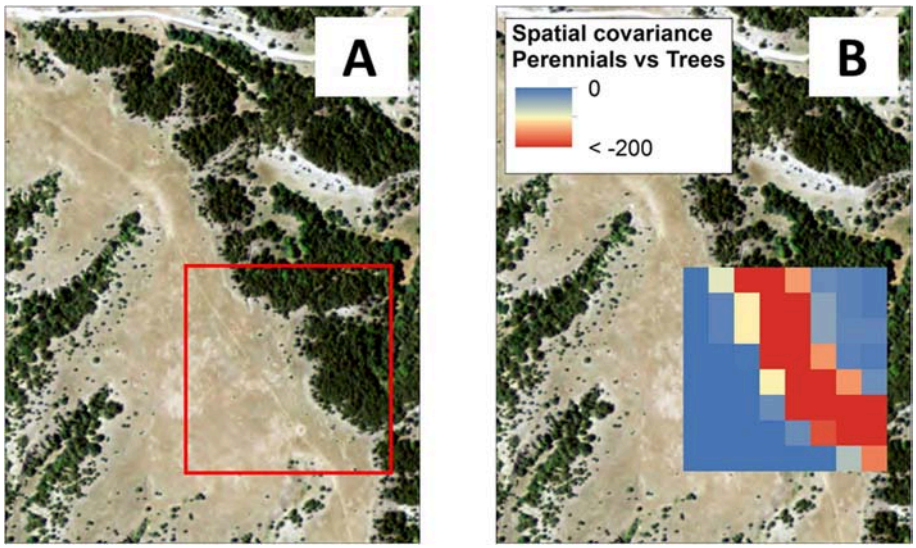

FIGURE 2 | (A) Landscape with visually apparent grass–tree boundaries and an example area (red box) for spatial covariance computation, and **(B)** The same landscape with perennial–tree spatial covariance mapped in the example area, where negative spatial covariance provides a regime shift signal associated with a lack of coexistence between perennials and trees (i.e., spatial regime boundary).

Screening Workflow

We screened for regime shifts by asking and answering five questions: (1) Which regime shift is expected or of greatest concern? (2) Can we detect a signal associated with the expected regime shift? (3) If detected, is the signal transient or persistent over time? (4) If detected and persistent, is the transition signal stationary or non-stationary (i.e., moving) over time? (5) What other signals do we detect while screening? The spatially explicit answers to these questions—each derived through spatial imaging—are useful for flagging locations for continued screening, as well as diagnostic testing and treatment by local experts, stakeholders, managers, and scientists. Whether a spatial transition signal is present vs. absent, persistent vs. transient, and non-stationary vs. stationary informs the screening–diagnosis–treatment decision (**Figure 3**).

Of the greatest concern are regime shift signals that are present, persistent, and non-stationary (i.e., moving). If signals are not persistent (i.e., transient), then they cannot be associated with regime shifts. This may be the case in instances where vegetation recovers in the wake of a disturbance. Another possibility is that vegetation signals persist through time but are spatially stationarity (i.e., do not spread), which is likely to occur along the geographic boundaries of opposing spatial regimes. Such places are also unlikely to be flagged as areas of concern during screening. Areas that are likely to be flagged as areas of concern are those that display spatially persistent and dynamic vegetation transition signals over time (i.e., non-stationarity). Such areas, where one spatial regime is actively displacing another, should be targeted for in-depth diagnosis of the change occurring (e.g., through remotely sensed imagery, monitoring, inventory, and local expert opinion) and/or treatment (e.g., management for preventing, halting, mitigating the effects of, or adapting to regime shift). Areas ahead of persistent and non-stationary transition signals (i.e., areas where change has not yet occurred but is likely to in the future) should be targeted for preventative management action, as they provide opportunities to anchor conservation efforts and build resilience against approaching regime shifts. The speed and degree of non-stationarity provide varying temporal windows for such vulnerability assessments and responses. Importantly, the targeting of areas for preventative management is predicated on the expectation that management is capable of preventing a given regime shift, which is not always true, particularly when dealing with broad-scale regime shift drivers (e.g., changing climatic conditions make the persistence of an established plant community below a given elevation unlikely, regardless of management) (Wonkka et al., 2019). For this reason, it is important to link screening results to management through a formal diagnosis of the regime shift and its likely causes. If management is incapable of preventing an approaching regime shift, then management resources and efforts may be more effectively devoted to transforming the system to mitigate the negative effects of the regime shift (Chapin et al., 2010; Chaffin et al., 2016; Garmestani et al., 2019).

We possessed varying degrees of knowledge about potential drivers of the spatial transition signals detected through screening in each of the focal landscapes. For illustrative purposes, we moved from screening to diagnosis by simply examining aerial imagery of focal landscapes and by speculating about potential spatial transition signal drivers. Further diagnosis could have been applied via on-site field inventory, monitoring, and analysis. In practice, there is a clear distinction between screening and diagnostic testing, so we avoid blurring screening

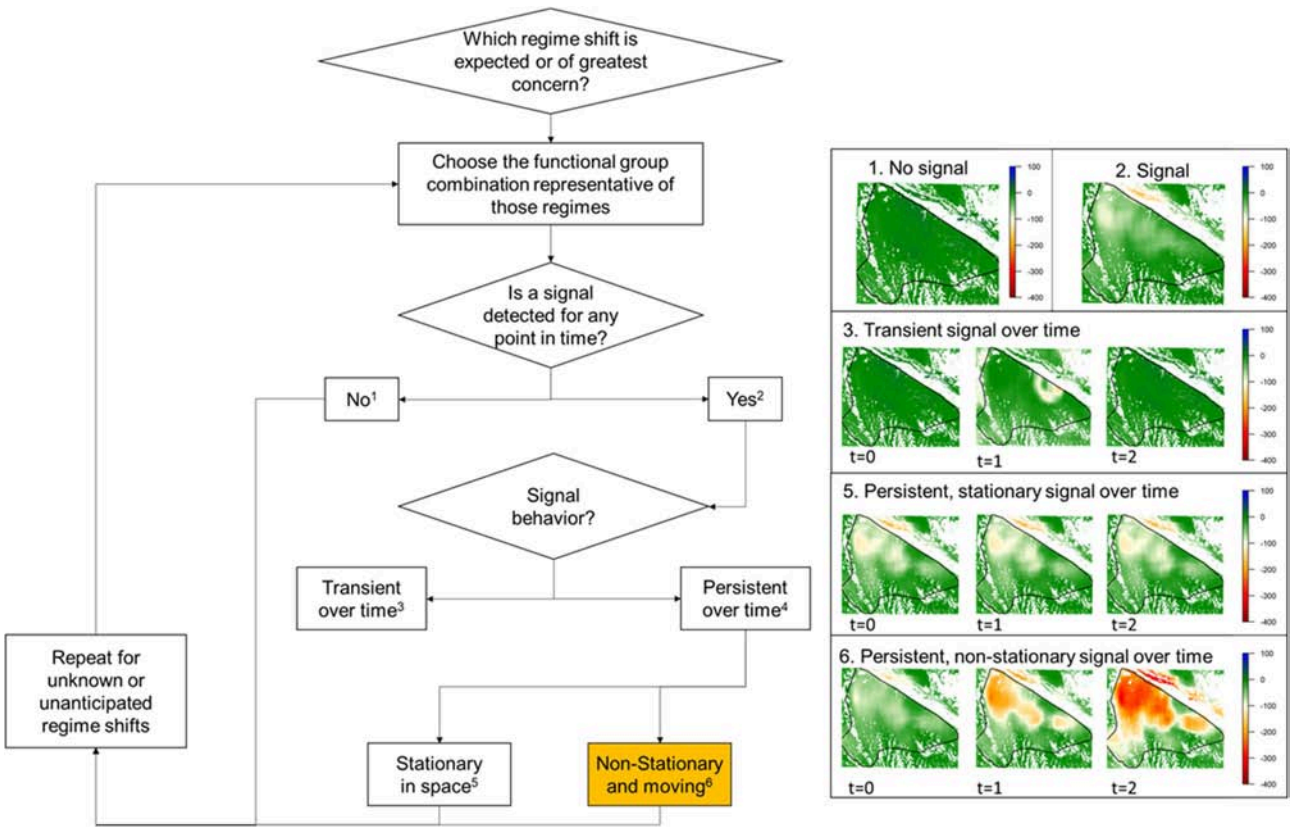

FIGURE 3 | Workflow for screening for vegetation transitions in ecological systems, according to spatial signal presence vs. absence, persistence vs. transience, and non-stationarity vs. stationarity over time. The yellow-color in box number 6 represents transition signals that are particularly concerning because of their temporal presence, persistence, and non-stationarity.

and diagnosis here except where a focal example required further investigation and explanation.

Focal Transitions and Landscapes

We screened for signals of the following three iconic rangeland vegetation transitions: (1) erosion and desertification; (2) woody encroachment; and (3) exotic annual grass invasion. Erosion and desertification involve shifts from vegetated to non-vegetated (i.e., bare ground) states; woody encroachment is a shift from grass-to-woody plant dominance resulting from the displacement of herbaceous perennial vegetation to shrubs or tree dominance; and exotic annual grass invasion is a shift from herbaceous perennials, shrubs, or trees to annual grasses. All of these spatial regime shifts, and the mechanisms by which they occur, are dependent on local contexts and differ across western USA rangelands. We therefore chose multiple study sites spanning the American Southwest, the Southern and Northern Great Plains, and the Great Basin to screen for spatial vegetation transition signals from 2000 to 2017. Each focal landscape is dominated by rangeland but possesses a unique environmental setting, species assemblage, disturbance history, and set of alternative regimes to which its rangelands may shift. Below, we overview briefly each of the three types of vegetation transitions and the focal landscape(s) we selected for screening.

Erosion and Desertification

Erosion and desertification are problematic phenomena that threaten human livelihoods in dryland rangelands worldwide and are therefore actively managed against (Bestelmeyer et al., 2015). In the United States, substantial investments are allocated each year to reducing erosion in order to avoid catastrophes like the Dust Bowl that accompanied the historic drought of the 1930s (Egan, 2006). We screened two landscapes with supposed heightened vulnerabilities to erosion and desertification: the Sandhills of north-central Nebraska and a cropped valley of the Mojave Desert of southwestern Nevada.

Nebraska sandhills

Large-scale erosion is a constant subject of concern in the Nebraska Sandhills—an ecoregion with sandy soils that are stabilized by perennial vegetation—particularly during wildfire and drought (Arterburn et al., 2018). At a smaller scale, blowouts (i.e., de-vegetated sand pits) are a common landscape feature throughout the Sandhills, but the spread of blowouts to neighboring grass-dominated areas is actively managed against, especially under dry conditions (Schmeisser

McKean et al., 2015). Using spatial covariance between bare ground and perennial forbs and grasses (hereafter perennials) functional groups in a moving window algorithm over a 27 by 27 pixel neighborhood, we screened for large-scale erosion and desertification in a Sandhills landscape centered around 42.8033°N and −100.0414°W in the years leading up to and following 2012, a year of extreme drought and in which the Region 24 Complex Wildfire occurred. At a smaller scale, we also used bare ground–perennial spatial covariance in a moving window algorithm over a 3 by 3 pixel neighborhood to screen for increased erosion in the vicinity of a randomly selected blowout centered around 42.7294°N and −100.0502°W within the Region 24 Complex Wildfire perimeter over the same set of years.

Mojave desert

Despite arid conditions, portions of the Mojave Desert support irrigated rowcrop agriculture; however, tilled soils are easily eroded and carried by wind into neighboring, non-tilled shrublands (Okin et al., 2001). Using spatial covariance between annual forbs and grasses (hereafter annuals) and bare ground in a moving window algorithm over a 9 by 9 pixel neighborhood, we screened for transition signals associated with erosion of croplands in a network of center-pivot irrigated rowcrop fields in southwestern Nevada centered around 37.7605°N and −118.0783°W.

Woody Encroachment

Woody plant encroachment threatens grasslands and savannas worldwide (Lasslop et al., 2016). In many systems, the dramatic shift in fire management associated with European colonization has facilitated the spread of woody plants into grasslands (Bowman et al., 2011). This class of regime shift demonstrates how disturbance regime alteration—in this case, severe reduction or elimination of historical disturbances—permits systems to advance to later successional trajectories with a high degree of spatial-temporal order. In other words, this regime shift is associated with lags in response to human-induced land management (Streit Krug et al., 2017). Herbaceous perennial species and woody plants tend not to coexist on a large scale in grasslands; therefore, woody encroachment results in a shift from herbaceous-to-woody plant dominance. We screened for transition signals associated with the encroachment of three woody species in two landscapes of the North American Great Plains: mesquite (*Prosopis* spp.) and ashe juniper (*Juniperus ashei*) in rangelands near the City of Breckenridge in north-central Texas and eastern redcedar (*Juniperus virginiana*) in rangelands of the Loess Canyons of west-central Nebraska.

North-central texas

Increases in mesquite cover have become a serious rangeland management challenge throughout much of northern Texas, with evidence that significant increases in mesquite cover can occur in treated (e.g., root-plowed) and untreated areas (Ansley et al., 2001). Using spatial covariance between perennials and trees in a moving window algorithm over a 27 by 27 pixel neighborhood, we screened for woody plant encroachment in a set of north-central Texas properties, near the City of Breckenridge, centered around 32.8635°N and −98.9537°W.

Nebraska loess canyons

The Loess Canyons landscape is located in southwest Nebraska, south of the Platte River, in the area centered around 40.9339°N and −100.5338°W. Steep hills and canyons are grazed for cattle production, but in recent decades, have rapidly experienced increases in eastern redcedar cover (Roberts et al., 2018b). We used spatial covariance between perennials and trees in a moving window algorithm over a 113 by 113 pixel neighborhood to screen for transition signals associated with shifts from grass-to-woody plant dominance in the Loess Canyons between 2000 and 2017.

Exotic Annual Grass Invasion

Over the past several decades, the exotic annual cheatgrass (*Bromus tectorum*) has rapidly invaded rangelands of the western United States, many of which were historically dominated by fire-intolerant shrubs and herbaceous perennial species. One of the major consequences of cheatgrass invasion has been fire regime alteration (D'Antonio and Vitousek, 1992; Balch et al., 2013; Chambers et al., 2019) and the emergence of a self-perpetuating annual grass/fire cycle. Cheatgrass changes fine fuel bed characteristics, resulting in larger and more frequent fires than would have occurred in uninvaded rangelands where fire was rare and spatially discontinuous. Reseeding is a commonly implemented management action for shifting vegetative dominance back from cheatgrass to perennials and to avoid further loss of sagebrush (*Artemisia* spp.) dominated areas to cheatgrass (Chambers et al., 2014).

Southeastern oregon

In a southeastern Oregon landscape centered around 42.3662°N and −117.8300°W, we used spatial covariance between annuals and shrubs in a moving window algorithm over a 27 by 27 pixel neighborhood to screen for transition signals associated with cheatgrass invasion and management. In this case, management included herbicide treatment to control brush and reseeding to an introduced perennial bunchgrass (crested wheatgrass; *Agropyron cristatum*) in the late 1960s (Heady and Bartolome, 1977). The management unit and surrounding landscape burned in the 2012 Long Draw wildfire.

RESULTS

Erosion and Desertification in the Sandhills

In the Nebraska Sandhills ecoregion, screening returned no evidence of large-scale erosion/desertification following the Region 24 Complex wildfire (**Figures 4A–D**). Although a stark signal that corresponded with the wildfire perimeter occurred in 2012 (**Figure 4C**), it vanished the following year and was therefore considered transient over time. From a practitioner's standpoint, we would conclude that no large-scale erosion or desertification is occurring, and therefore, the location could be flagged for continued screening, but neither additional diagnosis

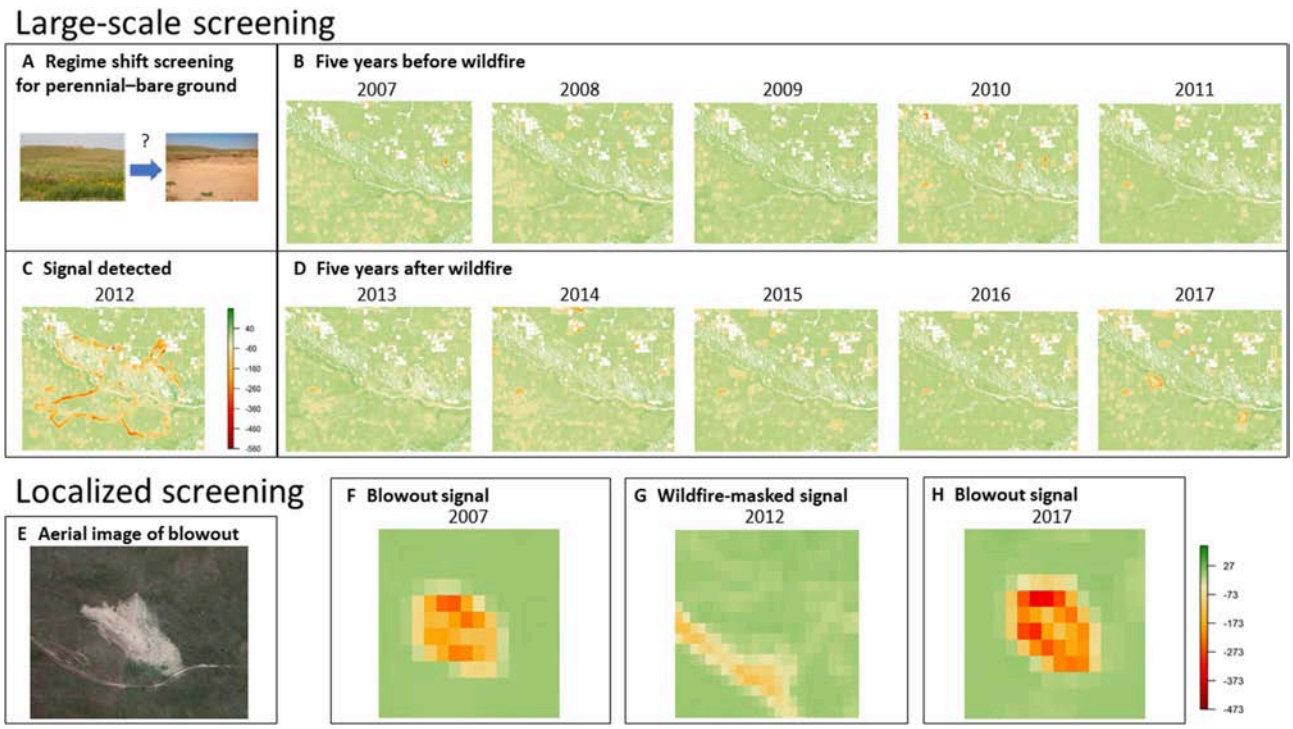

FIGURE 4 | Screening and spatial imaging for vegetation transitions following wildfire in the Sandhills of Nebraska, USA, during a severe drought. **(A–D)** Large-scale imaging at the extent of a 2012 wildfire perimeter; **(E–H)** local-scale imaging at the extent of a single blowout within the 2012 wildfire perimeter. Shown here are perennial–bare ground spatial covariance images, where more strongly negative spatial covariance values indicate increasing spatial incompatibility of the two functional groups at the relative scale of analysis.

(e.g., intensive field monitoring) nor expensive treatment (e.g., reseeding) are warranted. This conclusion is supported by a previous study that found rapid re-establishment and recovery of Sandhills prairie following the historic drought and wildfire (Arterburn et al., 2018).

An alternative explanation for the lack of a persistent, large-scale transition signal in the Sandhills landscape could be that erosion and destabilization are occurring at a finer scale of analysis but are not yet evident at the scale of the entire wildfire. When reviewing localized spatial signals, we detected a strong, persistent, and largely stationary bare ground–perennial signal that corresponded with a blowout within the wildfire perimeter (**Figures 4E–H**). The only notable change in the spatial transition signal representing the boundary between prairie and the blowout was in 2012 (**Figure 4G**), when the signal disappeared entirely from the blowout and moved to the wildfire perimeter. However, in the years following the fire, the bare ground–perennial signal associated with the fire perimeter rapidly faded and the signal associated with the perimeter of the blowout reappeared. Thus, from 2007 to 2017, the blowout's spatial transition signal was present and persistent, but it failed to exhibit non-stationary by spreading into surrounding areas—before, during, or after the wildfire—in a manner that led to the expansion of the blowout and displacement of perennial grassland. From a practitioner's standpoint, we would once again conclude that no additional diagnostic monitoring or treatment is warranted for this screening result. For illustrative purposes, we only analyzed a single, randomly-selected blowout for spatial transition signals of erosion and expansion; however, our approach could be used by a resource professional to monitor the entire networks of blowouts.

While screening for potential erosion and destabilization of the Sandhills prairie ecosystem, we also screened for spatial transition signals from other functional group combinations that might not have been expected (**Supplementary Figure 1**). At the large-scale, we detected a strong, persistent, and non-stationary spatial transition signal associated with perennial–tree spatial covariance over a 27 by 27 pixel neighborhood (**Figure 5**). This spatial transition signal corresponded geographically with the Niobrara River valley forest corridor. In the 5 years preceding the 2012 wildfire, the transition signal was present, persistent, and stationary (**Figure 5A**). However, there was a drastic shift in the spatial order of the signal following the wildfire that carried over into subsequent years (**Figure 5B**). This is indicative of a rapid and drastic collapse of a major portion of the riverine forest corridor, which included a mix of coniferous (ponderosa pine and eastern redcedar) and deciduous species. Local experts could use this information to focus their attention on the most pertinent regime shift occurring in this landscape, thereby avoiding overtreatment and potential misuse of funds because of a signal that will likely regain its intensity (recover) without human intervention, and hold in-depth discussions about the next steps needed to diagnosis the specifics of the regime shift and whether management intervention is necessary.

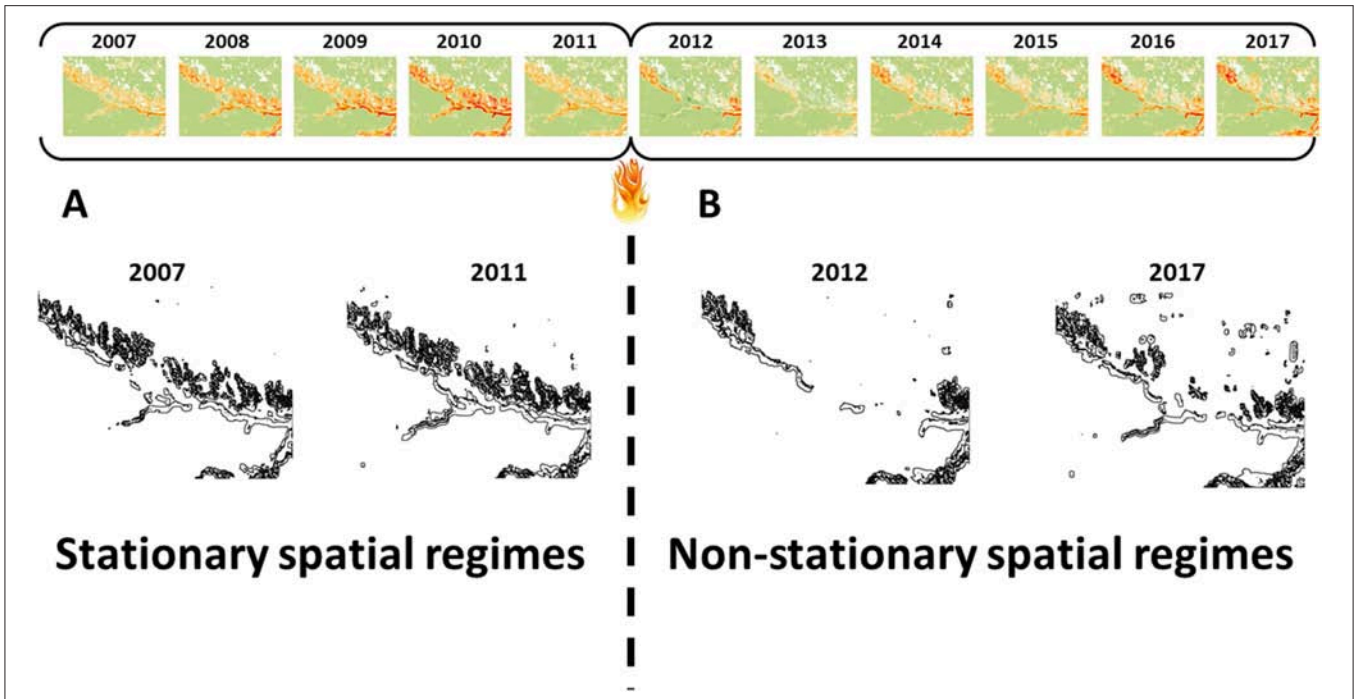

FIGURE 5 | Screening for additional vegetation transitions in the Nebraska Sandhills revealed **(A)** a present, persistent, and stationary large-scale perennial–tree spatial covariance signal from 2007 to 2011 and **(B)** a present, persistent, and non-stationary perennial–tree spatial covariance signal from 2012 to 2017, following the wildfire-induced collapse of the riparian forest corridor. More strongly negative spatial covariance values indicate increasing spatial incompatibility of the two functional groups at the relative scale of analysis Below, the outline of groups of pixels with perennial–tree spatial covariance of <100 in 2007, 2011, 2012, and 2017.

Erosion and Desertification in the Mojave

Persistent spatial transition signals associated with the individual perimeters of a network of center-pivot irrigated rowcrop fields were apparent in the Mojave (**Figure 6**). These persistent spatial transition signals remained stationary for many of the individual fields between 2003 and 2017 (**Figure 6A**), but non-stationarity was detected at other locations, where erosion is likely occurring and contributing to the desertification of adjacent lands. For example, in **Figure 6B**, the eastward bleeding of the spatial transition signal over time provides evidence of erosion and desertification. We did not detect any additional persistent spatial transition signals.

Woody Encroachment and Brush Management

Brush management for mesquite often results in a patch-work of properties with hard, stationary boundaries, where one property is dominated by perennial grass vegetation and the adjacent property is dominated by a mesquite shrubland. We were able to detect a transition signal for this type of boundary near Breckenridge, Texas (**Figure 7A**). Prior to 2008, a persistent and stationary transition signal was observed on an east–west line bisecting the landscape. We confirmed this to be two pastures separated by a fence-line *post-hoc*. The spatial transition signal became non-stationary in 2012. Aerial imagery for the years 2008, 2012, and 2017 revealed an increase in mesquite density and cover in the southwestern pasture over time that corresponded with the spatial transition signal, with the key implication being that an undesirable vegetation regime shift was detected and began to spread to areas previously dominated by perennial vegetation. Local in-depth diagnosis is warranted to determine why management is no longer holding the line, whether management has been discontinued, and how this regime shift can be prevented from continuing to expand into the surrounding rangeland landscape.

While screening for the expected and concerning spatial transition signal, we noted a secondary signal in the spatial covariance between bare ground and perennial functional groups over a 9 by 9 pixel neighborhood (**Figure 7B**). This signal appeared from 2011 to 2014 and exhibited markedly different patterns than in previous years. Further diagnostic investigation using aerial imagery over the same time period revealed that the spatial signal was associated with energy development and associated road infrastructure. Although the signal was the outcome of a purposeful, small-scale vegetation transition, this example shows how this rapid screening technique can image and track both known and unknown types of regime shifts occurring in rangelands, irrespective of whether shifts are of human or non-human origin.

Regional-Scale Juniper Encroachment

In the Loess Canyons ecoregion, we detected a strong, persistent, and directionally non-stationary spatial transition signal indicating a shift from grass-to-woody plant dominance (**Figure 8A**). A peak in the intensity of the spatial transition signal occurred from 2010 to 2011 and was followed by a

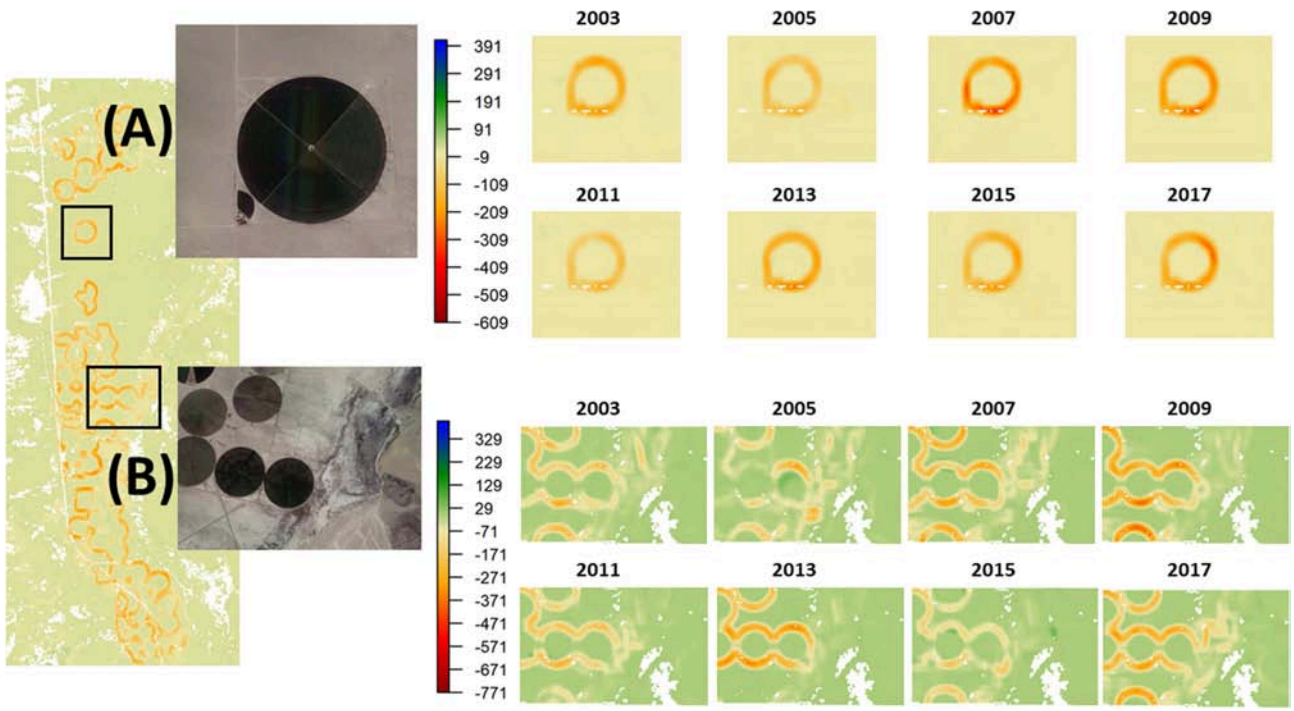

FIGURE 6 | Screening for spatial transition signals associated with erosion and desertification in a network of center pivot-irrigated rowcrop fields in the Mojave Desert every other year from 2003 to 2017, where more strongly negative spatial covariance values indicate increasing spatial incompatibility of the two functional groups at the relative scale of analysis, with examples of: **(A)** present, persistent, and stationary boundaries (i.e., no erosion/desertification); and **(B)** present, persistent, and non-stationary boundaries (i.e., erosion and desertification).

brief interruption from 2012 to 2014 (**Figure 8B**), after which directional change resumed and then plateaued from 2015 to 2017 (**Figure 8C**). The interruption of the spatial transition signal was likely the result of a severe drought in 2012 that differentially affected perennials and trees and briefly masked spatial associations driven by grass–tree interactions (i.e., strong negative spatial covariance), and the stabilization of the signal from 2015 to 2017 is presumably the result of large-scale, coordinated eastern redcedar management by a local prescribed burn association. No other persistent spatial transition signals were detected.

Cheatgrass Invasion and Management

We detected a persistent spatial transition signal with a geometry that corresponded to the boundary of a site with a history of wildfire and management against cheatgrass invasion (1960s herbicide treatment and reseeding to crested wheatgrass) in southeastern Oregon (**Figure 9**). Multiple transition signals were evident in the year preceding wildfire (2011), weakened in the year post-fire (2013) when vegetation was absent, and subsequently re-emerged or disappeared with vegetation recovery. The shrub–annual transition signal varied in intensity yet retained its overall spatial structure over time (**Figure 9A**). The emergence and disappearance of additional, localized shrub–annual transition signals in the vicinity of the original transition signal make it difficult to ascertain the degree to which the regime shift is spreading over time. It is likely the disappearance of these local signals corresponds with a loss of sagebrush and increase in annuals in the untreated landscape adjacent to the management unit following the 2012 wildfire. Similar overarching patterns emerged in the bare ground–annual (**Figure 9B**) and perennial–annual (**Figure 9C**) transition signals. The spatial covariance between perennials and annuals at the management unit border was slightly positive, which may be the result of cheatgrass replacing bare ground between bunchgrasses but not immediately replacing the bunchgrasses. Indeed, the strong negative spatial covariance between annuals and bare ground likely stems from the loss of bare ground in plant interspaces that accompanies transitions to cheatgrass. Therefore, these spatial transition signals may be collectively reflecting differences in the ability to resist cheatgrass invasion between the management unit dominated by perennial bunchgrasses and surrounding untreated lands. Additional on-site inventory and monitoring is needed to confirm the degree to which management has been successful at stemming cheatgrass conversion at this site and if regime shifts are occurring and spreading in the adjacent area. Analysis of temporal trends in data (e.g., detection of boom–bust cycles in the growth, spread, and interaction of annuals with other functional groups) may provide additional insights.

DISCUSSION

This paper explores the potential to image and screen for rangeland vegetation transitions. For a diverse set of

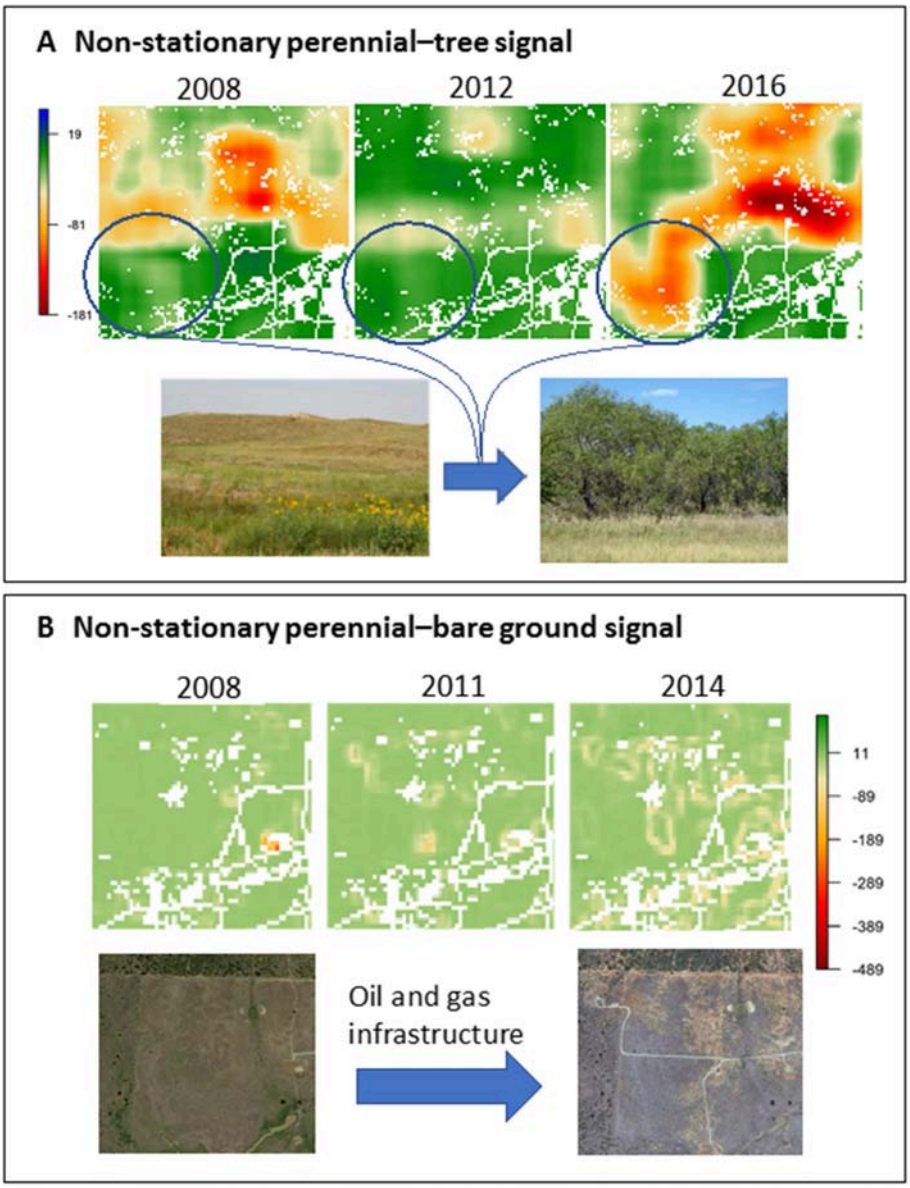

FIGURE 7 | Screening for spatial transition signals associated with woody plant encroachment near Breckenridge, Texas, where more strongly negative spatial covariance values indicate increasing spatial incompatibility of the two functional groups at the relative scale of analysis, with: **(A)** a present, persistent, and non-stationary perennial–tree spatial transition signal associated with woody encroachment from 2008 to 2016 and **(B)** the emergence of a present, persistent, and non-stationary bare ground–perennial spatial transition signal associated with energy and road development from 2008 to 2011.

rangeland-dominated landscapes of the western United States, we implemented a workflow (**Figure 3**) that: (1) identified the regime shift of greatest concern or that was most expected; (2) detected the presence of spatially explicit signals that were potential regime shift candidates; (3) differentiated transient signals of vegetation response from more persistent signals of vegetation transition over time; (4) determined whether persistent transition signals were stationary or non-stationary over time, and therefore, transitioning in space; and (5) repeat the process to screen for additional transitions in rangeland vegetation that were or lesser concern, not expected, or unknown *a priori*. This flexible methodology allows professionals to use spatial imaging to image spatial regime boundaries, track the magnitude and direction of regime shift signals, differentiate persistent and stationary transition signals from more-concerning persistent and non-stationary transition signals, and leverage disciplinary strength and resources for targeted diagnostic testing (e.g., inventory and monitoring) and treatment (e.g., management) of regime shifts. Because ecological systems experience frequent disturbances and are subject to

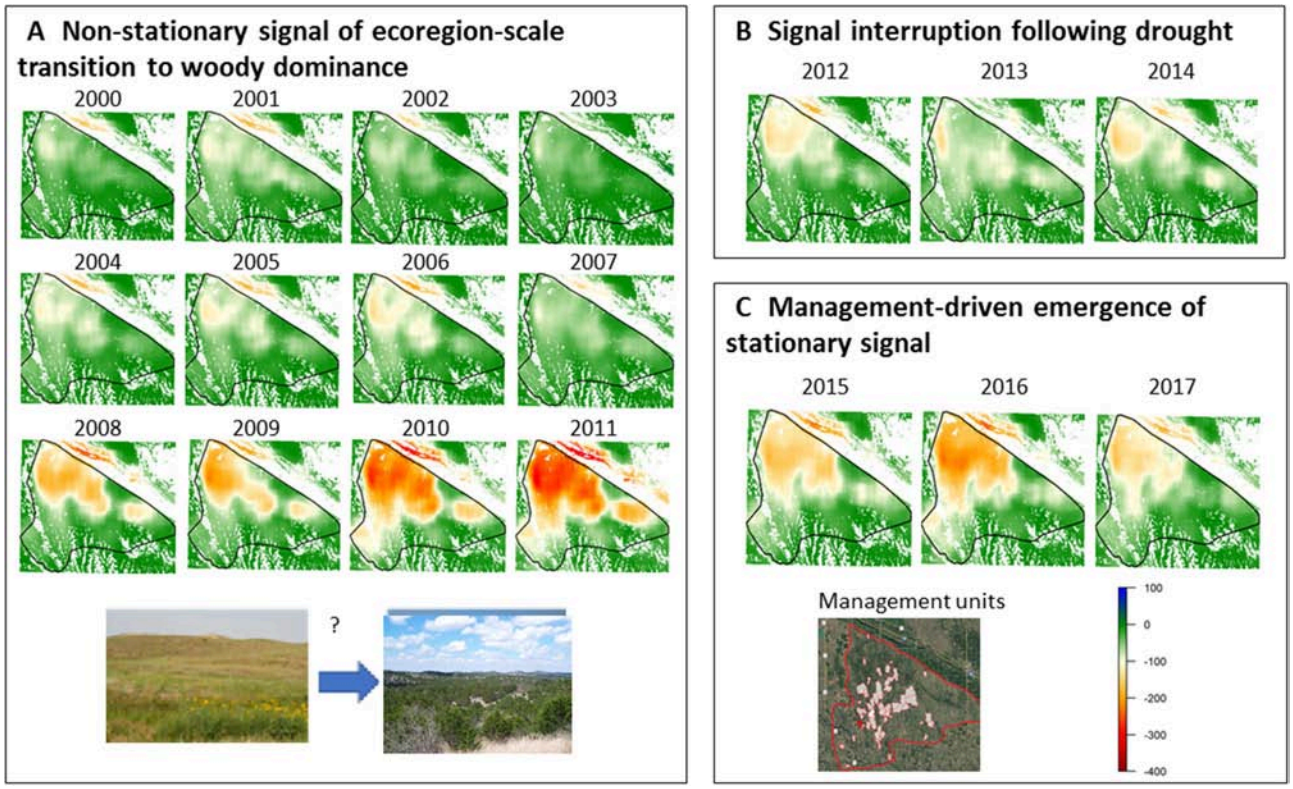

FIGURE 8 | Screening for spatial transition signals associated with woody plant encroachment in the Loess Canyons ecoregion of Nebraska, where more strongly negative spatial covariance values indicate increasing spatial incompatibility of the two functional groups at the relative scale of analysis, with: **(A)** a present, persistent, and non-stationary perennial–tree spatial transition signal from 2000 and 2011; **(B)** a brief interruption of the transition signal from 2012 to 2014 following historic drought; and **(C)** an increased and then management-driven stabilization of the transition signal from 2015 to 2017.

external forcing, screening for regime shifts—according to signal presence, persistence, and non-stationary—may help differentiate between temporary aberrations in conditions and major, possibly permanent, shifts.

Imaging and screening for regime shifts in ecology follows a similar logic to the mission of screening in medicine (Morris, 1994; Saunders et al., 2001), in that the consequences of such shifts are often so severe that it is in humanity's best interest to prevent the emergence of detrimental regime shifts or to treat them at the earliest possible point of detection. Many consequences of spatial regime shifts are unable to be predicted until after the shift occurs. Cheatgrass invasion and regional dominance led to surprising changes in wildfire behavior and occurrence, heightened exposure of urban populations to smoke and air pollution, and cascading impacts to endemic wildlife (D'Antonio and Vitousek, 1992; Balch et al., 2013; Chambers et al., 2014). Juniper displacement of prairie ecosystems in the Great Plains is now linked to concerning impacts on water resources (Zou et al., 2018), public school funding (Lally et al., 2016), wildfire suppression potential, and collapses in pastoral agricultural revenue and rural livelihoods (Twidwell et al., 2013a). Erosion and desertification has been a notorious regime shift that has been actively avoided since the tragedy of the Dust Bowl (Wallace and Silcox, 1936), which was driven in part by human conversion of rangeland to cropland.

Spatial metrics derived from resilience theory, next-generation data products, technological capabilities, and computational power have all advanced to the point where spatial signals of regime shifts can be imaged and tracked at geographic and temporal extents and resolutions that were previously infeasible. In the past, the computation and application of resilience theory metrics across large geographic extents and through time was logistically infeasible due both to data limitations and extreme computational requirements. Advances in geospatial cloud-computing have overcome such computational hurdles and have also contributed to recent advances in landcover data (Xie et al., 2019), including the data used in this study—continuous (i.e., not categorical) percent cover estimates for major functional groups at high spatiotemporal resolution (i.e., 30 m and yearly) and extent (i.e., western United States and multi-decadal) (Jones et al., 2018). Additional theory–data–technology linkages are foundational for the continued testing and application of resilience theory at multiple scales in ecological systems.

Moving forward, it is important to continue advancing regime shift screening with a guiding understanding of its strengths and limitations, which reflect those of screening in general. Regime

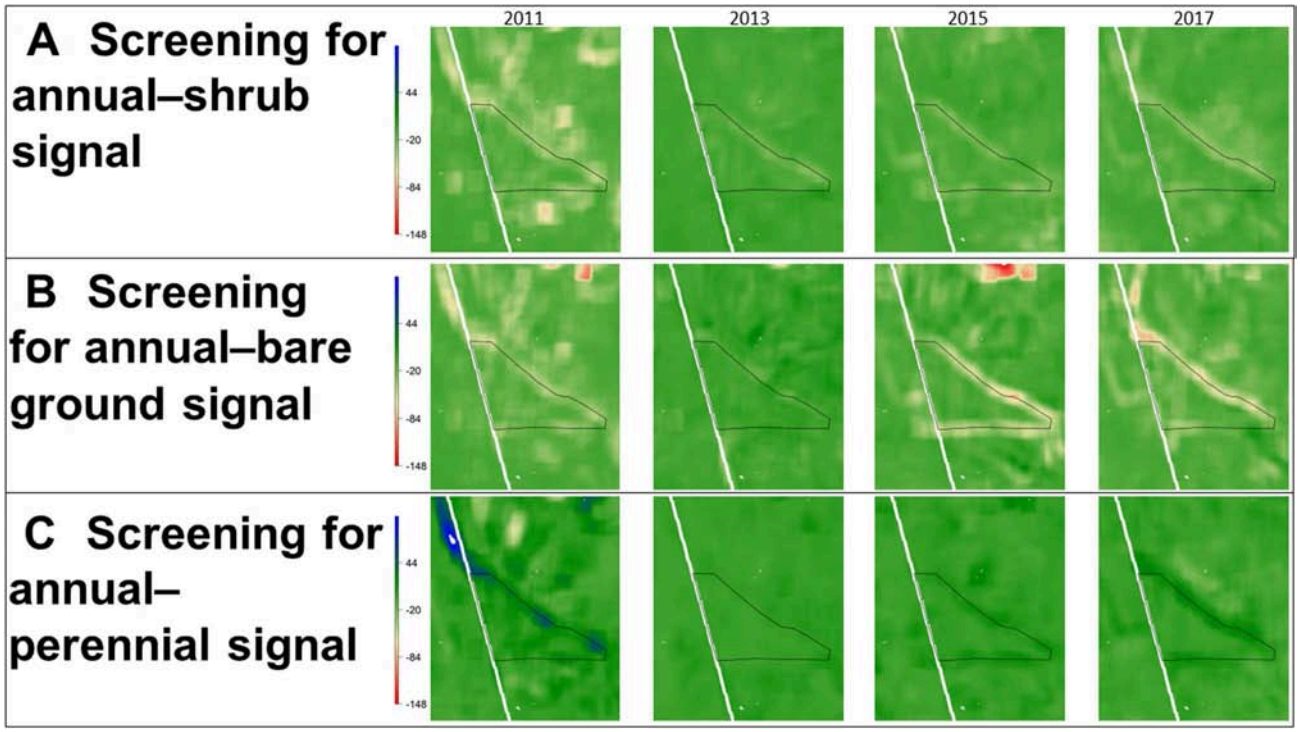

FIGURE 9 | Screening for spatial transition signals associated with exotic annual grass invasion in a southeastern Oregon landscape that experienced a 2012 wildfire, where more strongly negative spatial covariance values indicate increasing spatial incompatibility of the two functional groups at the relative scale of analysis. From 2000 to 2017, matching transition signals between **(A)** shrubs and annuals and **(B)** bare ground and annuals were present and relatively persistent and stationary. Over the same set of years, **(C)** a similarly-patterned perennial–annual spatial covariance signal (albeit slightly positive) between perennials and annuals was also evident. The management boundary is associated with the application of herbicide and reseeding with crested wheatgrass (*Agropyron cristatum*) in the 1960s (Heady and Bartolome, 1977).

shift screening may be most useful in circumstances where regime shifts have strongly negative consequences for people and the environment (Scheffer et al., 2001), when the scale(s) of policies match the scale(s) at which regime shifts are occurring (Cumming et al., 2006), and when there are established pathways between screening, diagnosis, and treatment. Alternatively, a general limitation of screening that should be addressed in future research endeavors is the susceptibility of screening to false positives. Here, the precautionary principle should be applied and candidate locations should be flagged for continued screening, diagnosis, and treatment, as it is arguably better to erroneously flag undesirable transition signals than to fail to detect them and be surprised by them. Additionally, the implementation of Holling and Allen (2002) adaptive inference could help minimize type II error (i.e., false negatives) during the initial screening stage and then subsequently reduce type I (i.e., false positives) through continued screening, diagnostic testing, and treatment. In diagnostic tests for regime shifts, spatial transition signals could also be paired with other sources of information (e.g., proportional cover of functional groups, Jones et al., 2018, vegetation inventory data, and local expert knowledge) to confirm the presence or absence of specific regime shifts. Regime shift screening may also benefit from comparisons with existing screening approaches, such as those based in medicine (Morabia and Zhang, 2004), environmental toxicity (Kramer et al., 2009), crop drought-tolerance (Tuberosa, 2012), and wildlife disease (Grogan et al., 2014). Such comparisons may also involve exploration of alternative screening metrics. We selected spatial covariance as a screening metric because of its alignment with ecology (Pielou, 1961; Goodall, 1965; Greig-Smith, 1983), complex systems theory (Norberg and Cumming, 2008), and spatial resilience theory (Cumming, 2011a,b; Allen et al., 2016). Although the primary focus of this study is the overall regime shift methodology, future studies should formally compare spatial covariance to alternative screening and diagnosis metrics with similar backings in resilience and complex systems theory. Such comparisons will be critical for extending and refining our approach to regime shift screening.

Using spatial imaging to screen for ecological regime shifts notably diverges from the existing and prevailing application of early indicators of regime shifts in ecology. Our approach to regime shift screening is not diagnostic and requires little-to-no *a priori* understanding of focal systems, their characteristic feedbacks, the disturbances they experience, or the alternative regimes to which they may shift. Many early warning indicators are largely diagnostic in their approach to undesirable transitions, as they focus on detecting change in its early stages (Biggs et al., 2009; Dakos et al., 2015) and require

extensive understanding of the focal system and its characteristic disturbances (Gsell et al., 2016). This has contributed to the tendency of ecosystem management to remain reactive instead of proactive in the present era of global change. Importantly, we do not disregard or devalue diagnostic approaches or place-based information, but instead emphasize the power of applying screening beforehand, at the front-end of the scientific process, as part of the overall mission of translating science to the general citizenship (**Figure 1**). Screening simply informs where to continue screening, diagnosing (e.g., inventorying), and treating (e.g., restoring and monitoring) at different points in time. Given the inherent spatial order of regime shifts, screening results can be used to prioritize locations in proximity to those exhibiting persistent and non-stationary transition signals for preventative management that builds resilience against the impending regime shift (Holling and Meffe, 1996; Chapin et al., 2010). Such locations have not yet experienced regime shifts, but are likely to in the future, and can therefore serve as areas for anchoring conservation efforts and building resilience against approaching regime shifts. Other locations in close proximity to regime shift signals may be prioritized for intensive management aimed at halting regime shift advance, while still other locations where regime shifts are already occurring at broad scales may be slated for adaptation-based management under the new regime (Chaffin et al., 2016; Garmestani et al., 2019). Local and expert sources of knowledge, as well as perspectives from social and political science, are essential for effective diagnosis and treatment of regime shifts, in order to better inform how screening results can be used to support decision-making and management.

Screening is widely applied to the early detection of undesirable change, and despite its utility in other fields (e.g., medicine) screening has not yet been introduced to ecological management. Meanwhile, under the increasing pressures of global change, ecological systems continue to experience shifts to alternative and often undesirable regimes (i.e., states). We developed a workflow for regime shift screening (**Figure 3**), which we used to screen for three of the most concerning transitions in rangelands: (1) erosion and desertification; (2) woody encroachment; and (3) annual exotic grass invasion. We screened for these transitions in an array of rangeland-dominated landscapes of the western United States—from the Mojave Desert to the Great Plains. Screening returned no evidence of regional-scale erosion/desertification in the Nebraska Sandhills following wildfire but did detect erosion in the vicinity of irrigated rowcrop fields in the Mojave. Screening also indicated local-to-regional-scale woody plant encroachment in several Great Plains landscapes and annual grass invasion in southeastern Oregon. While the screening approach outlined in this study is relatively new and unknown, it is well-grounded in the theories of ecology, complex systems, and spatial resilience, and as such, holds promise for the early detection of ecological regime shifts, particularly when effectively linked with strategies for regime shift diagnosis and treatment.

DATA AVAILABILITY STATEMENT

Data are available for visualization and analysis via the Rangeland Analysis Platform (https://rangelands.app/rap).

AUTHOR CONTRIBUTIONS

DU conducted the analysis and took the lead on writing. DT and DU conceived the idea. All authors contributed to writing and analytical design and development.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00407/full#supplementary-material

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METHODS
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Metrics and Models for Quantifying Ecological Resilience at Landscape Scales

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An explicit link between the abiotic environment, the biotic components of ecosystems, and resilience to disturbance across multiple scales is needed to operationalize the concept of ecological resilience. To accomplish this, managers must be able to measure the ecological resilience of current conditions and project resilience under future scenarios of landscape change. The goal of this paper is to present metrics and describe a process for using geospatial data, landscape pattern analysis and landscape dynamic simulation modeling to evaluate ecosystem resilience at management scales. The dynamic equilibria of species abundances, community structure, and landscape patterns that are produced under a given combination of abiotic conditions, such as topography, soils, and climate, can form a foundation to define desired conditions and measure resistance and resilience. The degree of forcing required to push the system from this dynamic range is a measure of resistance, and the rate of return to the dynamic range after the perturbation is a measure of the resilience and recovery of the system. Several tools from the field of landscape ecology are useful in defining the dynamic range of an ecosystem under natural regulation and to measure the forcing required to drive departure and the rate of recovery. Simulation models provide means to quantify the expected range of species abundance, community structure, and landscape patterns under a variety of scenarios, including the natural disturbance regime, current disturbance regime, and possible future regimes under alternative management and climate scenarios. Landscape pattern analysis and multivariate trajectory analysis provide a means to quantify conditions and change vectors relative to this desired range. Together this combination of tools provides a means to define the conditions of a desired state for an ecosystem, to quantify the degree of resistance and resilience of the system to perturbation, and to measure and monitor the departure from the range of natural variability in the system dynamics.

Keywords: landscape dynamics, FRAGSTATS, rmlands, landscape pattern analysis, resilience, recovery

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INTRODUCTION

Ecological resilience is a measure of the amount of perturbation required to change an ecosystem from one set of processes and structures to a different set of processes and structures, or the amount of disturbance that a system can withstand before it shifts into a new regime or alternative stable state (Holling, 1973; Curtin and Parker, 2014). In applied ecology, ecological resilience is also used

as a measure of the capacity of an ecosystem to regain its fundamental structure, processes and functioning despite stresses, disturbances, or invasive species (e.g., Hirota et al., 2011; Chambers et al., 2014a; Pope et al., 2014; Seidl et al., 2016). Much of the original literature on ecological resilience focused on theory, definitions, and conceptual ideas regarding resilience concepts (e.g., Gunderson, 2000; Folke et al., 2004, 2010; Walker et al., 2004; Gunderson et al., 2010). A major focus early resilience research was the importance of species diversity and species functional attributes related their response to stress and disturbance at local scales (e.g., Angeler and Allen, 2016; Baho et al., 2017; cf. Pope et al., 2014; Roberts et al., 2018). More recently research has focused on the ability of systems to maintain fundamental structures, processes, and functioning following disturbances (Folke et al., 2010). This so-called general resistance concept is now widely applied to evaluate responses ecosystems and landscapes, and to predict which systems are most vulnerable to transitions to alternative states (e.g., Hirota et al., 2011; Brooks et al., 2016; Levine et al., 2016), based on the relationships among an ecosystem's attributes and its responses to stressors and disturbances (Chambers et al., 2014a,b, 2017a,b).

Most relevant to this paper is the concept of spatial resilience, or how spatial attributes, processes, and feedbacks vary over space and time in response to disturbances and how they affect the resilience of ecosystems (Wu, 2013; Allen et al., 2016). Spatial resilience focuses on the capacity of landscapes to support ecosystems and biodiversity over time based on changes in landscape composition and configuration in response to disturbances (Frair et al., 2008; Keane et al., 2009; Olds et al., 2012; Hessburg et al., 2013; McIntyre et al., 2014; Tambosi et al., 2014; Rappaport et al., 2015).

The field of landscape ecology has developed a number of conceptual frameworks and modeling tools which underpin quantitative, spatial analysis of resilience (Turner, 1989; Wu and Loucks, 1995; McKenzie et al., 2011). The idea of dynamic equilibria of species abundances, community structure, and landscape patterns that are produced under a given combination of abiotic conditions, such as topography, soils, and climate, can form a foundation to define desired conditions and measure resistance and resilience (Romme and Knight, 1981). Specifically, under a given abiotic condition most ecosystems establish a dynamic equilibrium of species abundance, community structure and landscape patterns as a result of intrinsic competitive dynamics of the biological community interacting with the prevailing disturbance regime characteristic of that ecosystem in its topographical, edaphic, and climatic context (Turner et al., 1997). The dynamic equilibrium is an emergent property of the system under natural regulation and its characteristics can be used as state variables to define desired conditions. The degree of forcing required to push the system from this dynamic range is a measure of resistance and the rate of return to the dynamic range after the perturbation is removed is a measure of the resilience and recovery of the system.

Managing for ecological resilience requires a multiscale approach due to the nested, hierarchical nature of complex systems (panarchy; Holling, 1973; Wu and Loucks, 1995; Allen et al., 2016). Incorporating larger scales provides the basis for directing limited management resources to those areas on the landscape where they are likely to have the greatest benefit (Holl and Aide, 2011; Allen et al., 2016; Chambers et al., 2017c). Restoration efforts or conservation measures for individual species or small areas are often inefficient or unsuccessful if they do not consider the larger environmental context, pattern and process interactions, and essential ecosystem elements, such as biodiversity, habitat connectivity, and capacity to supply ecosystem services over time (Chambers et al., 2019).

To assess and manage ecological resilience managers need tools that can measure attributes of ecosystems relevant to resilience at scales larger than local measurements. Most research and monitoring of ecological systems and that related to resilience has focused largely on site measurements of soil, vegetation, water and other attributes measurable at points or in plots. However, much of the pattern-process dynamics of ecological systems occurs at scales of landscapes (Turner, 1989). Thus, it is essential that managers and scientists have methods to assess ecological conditions in landscapes, track them over time, and project changes under alternative scenarios. This is particularly true in the context of managing public lands in the Western United States, given the rapid changes in disturbance regimes and resulting ecological conditions resulting from the interaction of rapid climate change (Littell et al., 2018) and the legacy effects of past fire suppression (Baker, 1992; Kotliar et al., 2002).

The United States public lands agencies, most notably the US Forest Service, have been pioneers in adopting a landscape-scale approach to natural resources management, and now operate under an adaptive management paradigm in which desired conditions that are intended to reflect resilient and sustainable ecological states are defined, management is implemented to move the landscape toward those desired conditions, and monitoring is conducted to track the effectiveness of management in achieving those desired conditions. However, adaptive management, as implemented by the US Forest Service, has been limited due to administrative, technical and financial obstacles. This has resulted in a piecemeal, inconsistent and often inefficient application of the concepts. Most critically, US natural resource agency applications of landscape management have not widely adopted quantitative spatial analysis to assess current landscape conditions, nor have they frequently linked them with spatial simulation modeling efforts to project conditions into the future under alternative scenarios and altered disturbance regimes. Without quantitative spatial assessment and projection of future changes it is difficult to assess current conditions or to choose among alternative management scenarios based on expected impacts on future ecological conditions.

This paper describes landscape-level approaches to measure and track ecological conditions relative to management goals or resilience ranges/targets. We discuss how managers can link these spatial assessments to landscape modeling to project ecological dynamics into the future under novel stressors and disturbance or successional regimes.

Landscape dynamic simulation modeling provides means to quantify the expected range of species abundance, community structure and landscape patterns under natural regulation (e.g.,

Costanza and Voinov, 2004; Littell et al., 2011). Tools such as landscape pattern analysis (McGarigal et al., 2012), direct and indirect community ordination (TerBraak and Prentice, 1988; Cushman and McGarigal, 2002; Ohmann and Gregory, 2002), and multivariate trajectory analysis (Cushman and McGarigal, 2007) provide a means to quantify conditions and change vectors relative to resilient desired conditions. Together this combination of tools provides a means to define the conditions of a desired state for a healthy ecosystem and to quantify the degree of resistance and resilience of the system to perturbation, and to measure and monitor the departure from these conditions relative to the range of natural variability in the system dynamics.

This paper is organized around an example of operationalizing these ideas at the scale of a large landscape. The sections below introduce the case study area and the scope and focus of the assessment, present ways to use landscape pattern analysis to assess the composition and configuration of the case study landscape, and then introduce the use of spatially explicit, dynamic landscape simulation modeling to assess the perturbation of the system from the range of variation under a natural disturbance regime, and use landscape pattern analysis and trajectory analysis to evaluate the extent and nature of departure of the case study landscape from the historic range of variability.

In this study we use departure of landscape structure from ranges expected under a natural disturbance regime as a measure of perturbation of the ecosystem, with the assumption that the range of natural variation represents resilient conditions that support natural ecological processes and that the degree of departure is a measure of perturbation or reduction in system resilience. The degree to which and the time needed for the landscape to recover to within this range is a measure of ecosystem capacity to recover. It is important to note that this is a single example focusing on landscape patterns in comparison to dynamic ranges under historic disturbance regimes. This example is not exhaustive in terms of representing all the aspects of resilience and recovery that are relevant in ecosystems at the landscape level. It is chosen to illustrate tools, in particular multivariate analysis of landscape pattern statistics and landscape dynamic simulation modeling, which can be employed to assess ecosystem structure, function, resistance and recovery at a range of spatial and temporal scales in relation to a range of pattern-process relationships. Ecological resilience and desired conditions should be assessed relative to meaningful, quantitative and specific benchmarks. We chose to use dynamic ranges under historic disturbance regimes as a conceptually accessible approach to using landscape pattern analysis and simulation modeling to assess landscape condition and trend relative to desired conditions. However, in practice historic landscape dynamics prior to major human perturbations are often not particularly realistic given the rapid, global alteration of ecological conditions (Crutzen, 2006; Hobbs et al., 2009). In practice, therefore, we recommend managers and analysts develop desired conditions based on process-based assessments of ecological system structure and function. The historic range of variability of landscape conditions, in that context, often will not define desired conditions, but usually will still remain highly relevant as a benchmark or reference framework to assess current system and future system characteristics, drivers and dynamics (McGarigal et al., 2018).

OVERALL STRUCTURE OF APPROACH

Before going into the details of the particular case study example, it may be useful to provide a broad, conceptual overview of the approach, its components, and how these are integrated. **Figure 1** is a conceptual diagram showing the main steps of this approach. The boxes represent tools, circles represent inputs, outputs or outcomes, and the arrows represent applications and connections of the tools. The analysis can be run in two "directions." First, modeling and landscape pattern analysis can be used to assess the current condition relative to a reference framework, such as simulation of landscape pattern and dynamics under a historic disturbance regime (**Figure 1A**). That can be one way to inform the development of a "desired condition" that management will try to achieve. Once the desired condition is specified, the modeling approach can be run to evaluate how alternative scenarios of management, climate change, altered disturbance regimes and other factors affect the trajectory of landscape change toward or away from that objective, and to select the optimal scenario that most effectively meets management objectives (**Figure 1B**).

The example presented below combines these two approaches, by first using simulation modeling to define the dynamic range of landscape conditions expected under the historic disturbance regime, assessing the current landscape departure from that range of conditions and then evaluating how readily the landscape can return to those conditions if the historic disturbance regime were reinitiated. As noted above, this is a simplified example for heuristic purposes. In practice, managers would likely be better served by defining desired conditions based on more sophisticated assessments of resilience than historic ranges of variability, such as evaluating how a range of species, ecological conditions, and disturbance processes interact to affect system dynamics and stability. Furthermore, a more sophisticated approach to scenario evaluation should typically be used, in which a range of realistic alternative management scenarios, in the context of potentially changing climatic and disturbance drivers, interact to affect landscape conditions relative to these resilience goals (e.g., Kaszta et al., 2019). McGarigal et al. (2018) is perhaps the most complete and robust current example of combining both of these components in evaluating resilience of large forested landscapes and comparing alternative management scenarios to achieve desired conditions.

PROJECT AREA DESCRIPTION

The case study landscape is located in western Montana and northern Idaho, USA, and encompasses portions of the Lolo, Idaho Panhandle, and Kootenai National Forests, and the Flathead Indian Reservation. It is a logical ecological unit encompassing 1,827,400 ha and three subsections (Coeur

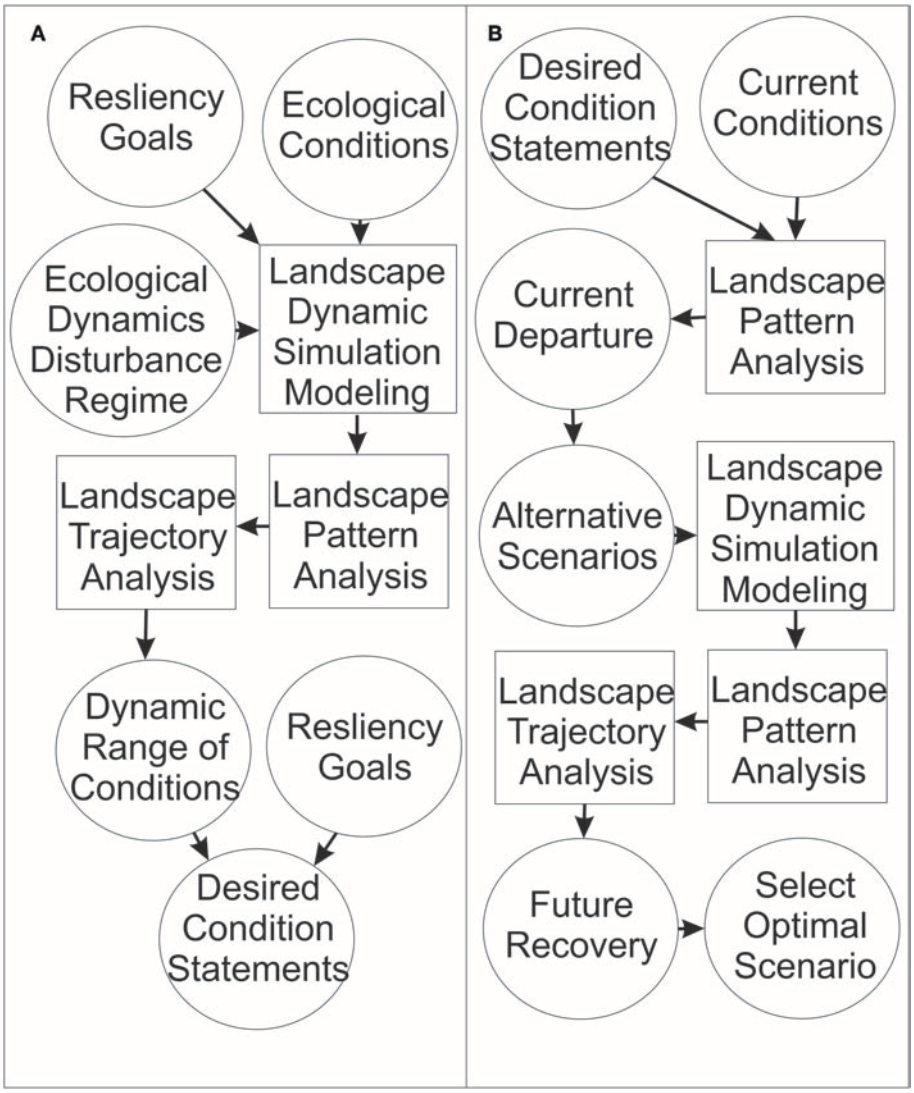

FIGURE 1 | Conceptual diagram of applying landscape pattern analysis, landscape dynamic simulation modeling and landscape trajectory analysis to assess resiliency goals and desired conditions. Circles represent inputs or outputs of the analysis. Boxes represent analytical steps. Arrows represent linkages between inputs, analysis and outputs. **(A)** Shows the steps in a process of producing quantitative, detailed and specific desired conditions statements from a priori resiliency goals. **(B)** Shows the process of evaluating alternative scenarios given a priori detailed, specific and quantitative desired condition statements.

d'Alene Mountains, St. Joe-Bitterroot Mountains, and Clark Fork Valley and Mountains) in the Bitterroot Mountains section (**Figure 2**).

There are many agents of pattern formation at the scale of the case study landscape. At more than 1.8 million hectares in size, the case study landscape contains a diverse physical environmental template, including dramatic gradients in moisture, temperature, and vegetation driven largely by variability in landform and climate. Vegetation communities and how they are distributed along environmental gradients provide the dominant source of coarse-scale landscape pattern and have a profound influence on most ecological processes and the distribution and abundance of species. Landscape dynamics in the case study landscape are driven by several coarse-scale disturbance processes such as wildfire and bark beetle outbreaks (e.g., mountain pine beetle) that interact with the physical template and each other to significantly affect vegetation patterns. Human land use patterns, past and present, also exert powerful controls on vegetation. Urban and agricultural development, largely in the low-lying valley floors, and industrial land uses such as mining and the associated transportation infrastructure (i.e., roads) create patterns that can affect the function of the landscape, in particular by disrupting habitat suitability and connectivity for wide-ranging organisms. In addition, forest management practices associated with timber harvesting and fire suppression have altered the spatial pattern of vegetation seral stages across the landscape.

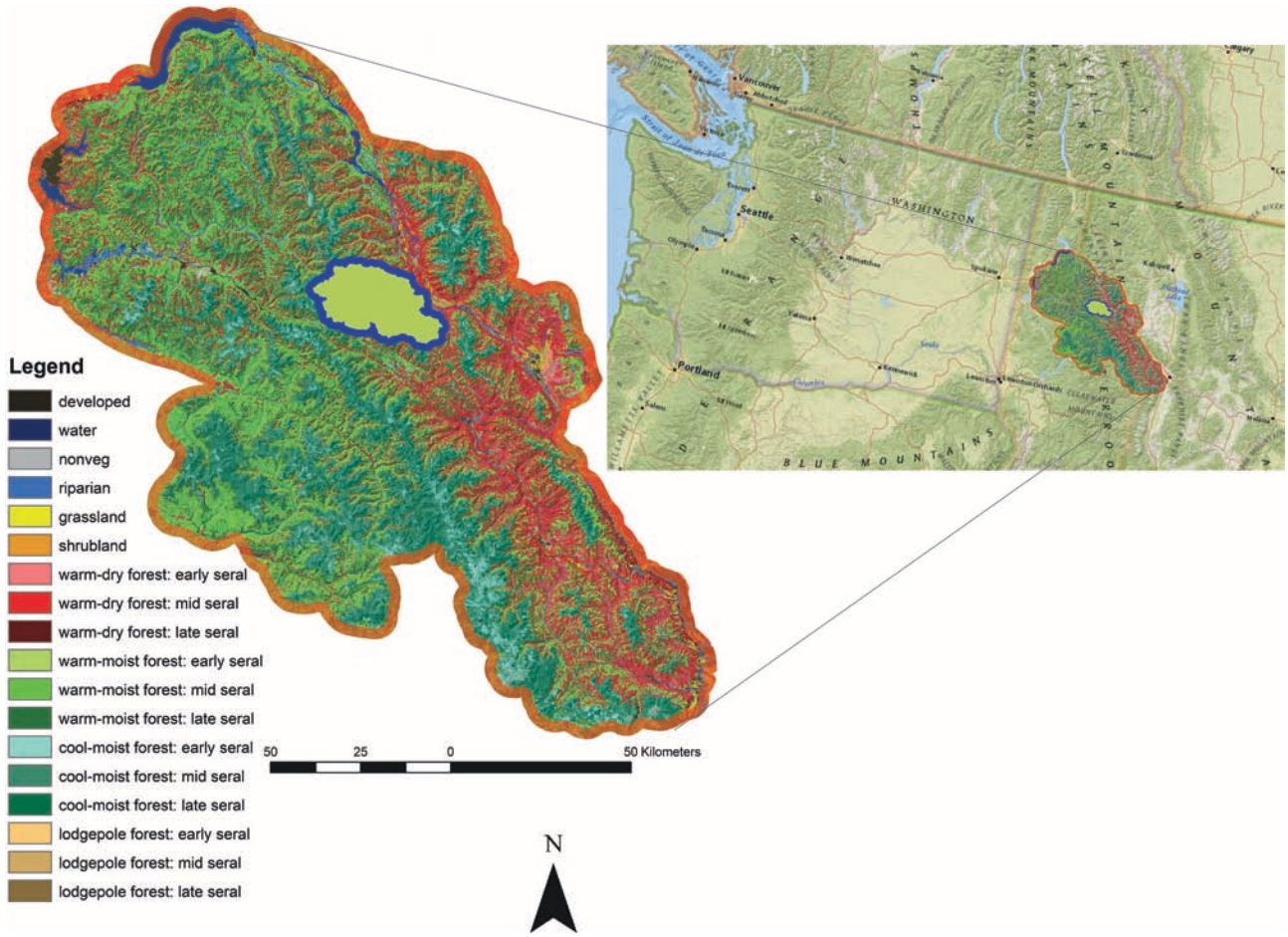

FIGURE 2 | Study area orientation map. The case study landscape consists of a natural ecological unit in the Bitterroot Mountains of Idaho and Montana, USA (inset landscape with orange border). The Prospect Creek sub-landscape, where much of the spatial analysis is illustrated is shown as a green polygon with blue border.

LANDSCAPE DEFINITION

The next step after defining the case study landscape is to select an appropriate landscape definition to represent patterns and their relationships to processes. This step has many important considerations (Cushman et al., 2013). Our analysis uses the landscape mosaic model (Forman and Godron, 1981), since it is by far the most commonly employed conceptual model and most landscape analysis tools use this framework. However, it is important to consider the implications of choosing the patch mosaic approach in terms of what patterns can be represented and how they can be related to driving processes. Often a gradient representation of patterns and processes can be more realistic (e.g., McGarigal and Cushman, 2005; Cushman et al., 2010), but is often limited in applicability due to lack of landscape pattern and landscape simulation tools that operate in a gradient-based framework.

Given the framework of the landscape mosaic model, we must first decide on the thematic content and resolution of the map (Buyantuev and Wu, 2007) as well as its spatial resolution (i.e., grain and minimum mapping unit; Turner, 1989; Wu, 2004). These decisions are constrained by available GIS data, the extent of the landscape, and the objectives of the analysis. There are nearly an unlimited number of variations in landscape definitions, which can have important implications for landscape analysis (Buyantuev and Wu, 2007). For heuristic purposes, we shall consider only one landscape definition in the analyses below. However, it is essential to realize that how the landscape is defined in terms of grain, extent, thematic content and thematic resolution completely controls the patterns that are measured and their relationships to underlying processes and to the concepts of resistance, resilience and recovery.

The landscape definition chosen for this analysis has the following attributes. *Thematic content*—The thematic content of our landscape definition is a raster map representing a patch mosaic of vegetation cover types with large streams and all roads overlaid. *Thematic resolution*—The thematic resolution of our land cover map is defined by the combination of two factors: (1) vegetation cover type, (2) condition, which is essentially seral stage and canopy closure. The cover type map is taken

from Landfire (Rollins, 2009) and includes 22 cover types plus human development classes of road, agriculture, urban, and water. Condition has eight classes as follows: non-seral, early-all structures, mid-all structures, late-all structures, mid-closed, mid-open, late-closed, late-open. The final covercondition (covcond) map used for measuring and modeling landscape patterns therefore consists of the combination of 22 cover types at each of the eight condition classes. The spatial resolution of all raster maps is 30 m. We ran spatial filtering to specify a minimum mapping unit of patches of at least 4 cells in extent, to remove the salt-pepper effect of small and inaccurately identified patches, which can negatively impact landscape pattern analyses.

For the example analyses presented here we have chosen a subbasin within the case study landscape (**Figure 3**). Prospect Creek Basin is a 47,058 ha watershed in the Lolo National Forest of western Montana (Cushman et al., 2011). We chose this landscape because a regional landscape analysis of biophysical characteristics identified it as highly representative of the surrounding 1,827,400 ha comprising three subsections (Coeur d'Alene Mountains, St. Joe-Bitterroot Mountains, and Clark Fork Valley and Mountains) of the Bitterroot Mountains Ecosection. The covercondition classes used in the analyses below are the intersection of these the cover type and seral stage classifications. We show them individually here given the difficulty of interpreting maps with many classes, but it is important to keep in mind that the analysis is done on the intersection of these two, producing 22 covercondition classes.

MEASURING LANDSCAPE PATTERN

The next step is to quantify landscape patterns for the case study landscape and describe its structure and composition. This step involves using the landscape pattern analysis program FRAGSTATS (McGarigal et al., 2012). Given the need for brevity, we focus on the results of this landscape pattern analysis. However, choice of landscape metrics is critically important and it is essential that researchers and managers understand metric parsimony (Cushman et al., 2008) and behavior (Neel et al., 2004), as well as how different landscape metrics may be related to ecological processes of interest, such as species distributions (Grand et al., 2004; Chambers et al., 2016) or connectivity (Cushman et al., 2012, 2013).

Landscape structure consists of several attributes measuring landscape composition (the abundance and variety of landscape

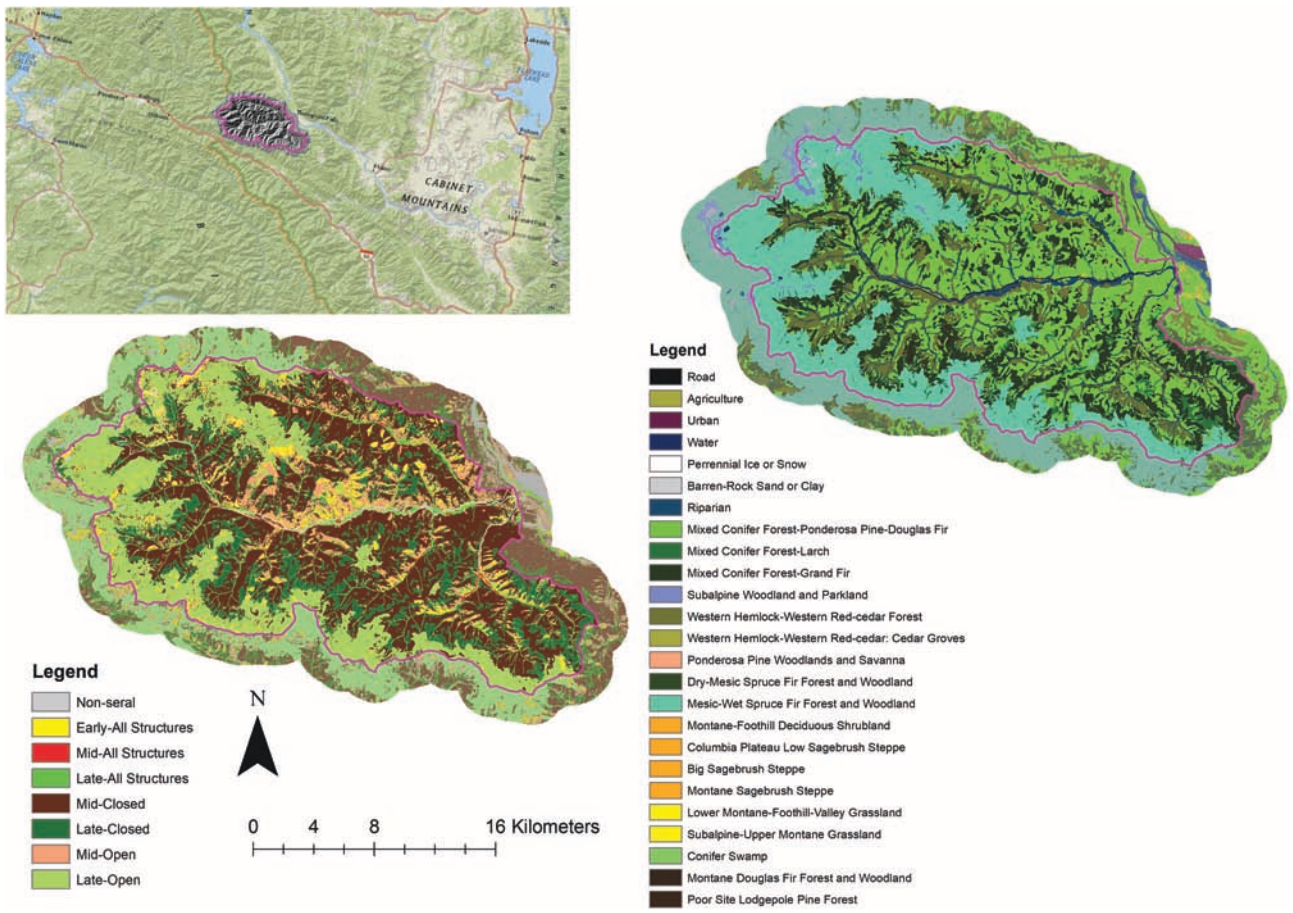

FIGURE 3 | Prospect Creek sub-landscape. The panel in upper left of figure shows the location of the Prospect Creek watershed. The panel in the lower left shows the seral stage mosaic of the watershed, while the panel in the upper right shows the vegetation cover type mosaic of the watershed.

elements) and landscape configuration (measuring the pattern and configuration of landscape elements). Generally, for most ecological processes landscape composition has larger effects than landscape configuration (e.g., Fahrig, 2003; Mateo-Sanchez et al., 2014). However, landscape configuration is particularly important for spatial processes, such as disturbance initiation and spread, and dispersal and colonization (Cushman et al., 2012), which are often the focus of assessments and analyses of ecological resilience. Therefore, we strongly suggest analysts consider several of the main aspects of landscape configuration (Cushman et al., 2008), such as edge contrast, patch shape complexity, aggregation, patch proximity/nearest neighbor, and large patch dominance, in addition to landscape composition. For this illustration it is not important to fully understand the intricacies of each metric. Instead, we focus on a few metrics that have intuitive interpretation.

LANDSCAPE DYNAMIC SIMULATION MODELING

The example presented here focuses on analyses of historic range of variability (HRV) of landscape structure under a natural disturbance regime, the departure of the current landscape from that range, and the degree to which return to natural disturbances could lead to recovery of resilient landscape patterns. We use a landscape disturbance-succession model (LDSMs, Mladenoff and Baker, 1999) to quantify HRV. In this paper, we present the results of the Rocky Mountain Landscape Simulator (RMLands, Cushman et al., 2011; McGarigal et al., 2018) to quantify HRV for the Prospect basin study area. Because we are using an LDSM to quantify HRV, we will refer to the "simulated range of variation" (SRV) instead of HRV to highlight the fact that our determination of HRV is based on a simulation and therefore subject to the limitations of the model.

RMLands Overview

RMLands is a grid-based, spatially-explicit, stochastic landscape simulation model designed to simulate disturbance and succession processes affecting the structure and dynamics of Rocky Mountain landscapes. RMLands simulates two key processes: succession and disturbance. These processes are fully specified by the user via model parameterization and are implemented sequentially within user-specified time steps for a user-specified period of time. Succession occurs at the beginning of each time step and represents the gradual growth and/or development of vegetative communities over time. Succession is implemented using a stochastic state-based transition approach in which vegetation cover types transition probabilistically between discrete states (conditions). Transition pathways and rates of transition between states are defined uniquely for each cover type and are conditional on several attributes of a vegetation patch.

Model Characteristics

RMLands can be classified as a hybrid statistical/probabilistic model with the following distinguishing characteristics: (1) RMLands utilizes a grid-based data model in which the landscape is represented in a regular grid lattice structure. Each grid cell (pixel), representing a fixed geographic area, possesses a number of ecological attributes (e.g., cover type, age). Attributes possess multiple states (i.e., unique values), many of which change over time in response to succession and disturbance. (2) Consistent with the grid structure, RMLands is a spatially-explicit model; grid cells are geographically explicit and topological relationships are important in all processes (e.g., disturbance initiation and spread). (3) RMLands is a process-based model and simulates both disturbance and succession. Disturbance processes include a variety of both natural and anthropogenic disturbances that are implemented in a common fashion. Succession is based on a discrete state transition model for each cover type. (4) RMLands is a stochastic model. Each cell has a probability of initiation for each disturbance process that is contingent on several cell attributes. Thus, given the same cell attributes, some cells will initiate while others will not. There is a stochastic element to nearly all processes in RMLands. (5) The grid can be defined at any spatial resolution, although current applications utilize a relatively high resolution (25–30 m cell size) grid that allows for detailed representation of landscape patterns. In addition, while RMLands does not limit the extent of the landscape, it is most applicable to landscapes between 10,000's ha to over 1 million ha. (6) RMLands operates on a user-specified time step and is most applicable to simulating landscape dynamics over 100's to 1000's of years.

STEPS OF ASSESSING SRV AND CURRENT DEPARTURE RELATIVE TO ECOLOGICAL RESILIENCE

This example focuses on using landscape pattern analysis and landscape dynamic simulation modeling to evaluate the resilience of a case study landscape. The evaluation is based on quantifying current landscape structure and comparing it to the ranges of landscape patterns simulated under a natural, historical disturbance regime. The link to resilience is the idea that the structure of the landscape (composition and configuration) that emerged under the natural historic disturbance regime reflects the dynamics of the landscape under regulation by natural processes and the conditions under which ecological processes and species existed prior to perturbation by human influences. The assessment example is presented in five steps, which are described below.

Step 1. Establish the Objective of the Analysis

The first step is to establish the objective of the analysis. Our overall objective is to quantify HRV for the sample landscape and compare the current landscape departure from it to assess some aspects of ecological condition relevant to resilience, and evaluate how readily the landscape can recover from this departure if the natural disturbance regime were reimposed, as a measure of recovery. We focus on three questions: (1) What is the historic range of variation in landscape structure in the sample landscape? (2) What is current degree of departure of the current landscape

condition from that historic range of variability, and how do these things change with the spatial scale (extent) of the landscape under consideration? (3) How readily does the landscape pattern recover to within the HRV after the reimposition of the historic disturbance regime.

For the purpose of this example we define "historic" as the period from about 1300 to the late 1800s, representing a period of largely *indigenous settlement*. This period represents a time when broad-scale climatic conditions were generally similar to those of today, but Euro- American settlers had not yet introduced the sweeping ecological changes that now have greatly altered many Rocky Mountain landscapes. Moreover, it was a time of relatively consistent (though not static) environmental and cultural conditions in the region, and a time for which we have a reasonable amount of specific information to enable us to model the system.

Step 2. Define the Digital Landscape

The next step is to define the digital landscape. We selected a single sample landscape (Prospect Creek Subbasin), from the entire case study landscape based on the following criteria: (1) landscape extent large enough to incorporate meaningful landscape dynamics given the scale of the major disturbance processes, yet small enough to be computationally efficient for lab use, (2) representativeness of the major land cover patterns found throughout the entire case study landscape; in particular, focusing on adequate representation of the four dominant forest cover types, (3) a heterogeneous mixture of land use practices, including developed lands with a wildland-urban interface, a mixture of public and private lands dominated by the former, and an adequate road network to facilitate future vegetation treatments, and (4) a logical ecological unit, in this case, a watershed, meeting the above criteria. Based on these criteria, we selected Prospect Creek basin, a 47,058 ha watershed located roughly in the center of the case study landscape (**Figure 3**).

We classified the sample landscape into land cover classes based on the LANDFIRE project (Rollins, 2009). Specifically, land cover classes represent unique biophysical settings (BpS) or potential vegetation types (PVT). The only significant change we made to this classification scheme was to combine three separate BpS classes corresponding to "riparian" settings into a single "riparian" class. The spatial grain (or resolution) of the landscape was set at 30 m, consistent with the spatial resolution of the data sources used in the LANDFIRE project. The spatial extent of the landscape was based on the hydrological watershed of Prospect Creek, a tributary of Clark Fork River; however, for simulation purposes we included a 2-km wide buffer zone around the basin, bringing the total extent of the simulation landscape to 69,293 ha.

Step 3. Run the RMLands Simulation and Quantify the Structure of the Simulated Landscapes Using FRAGSTATS

The next step is to parameterize and run the RMLands simulation and then parameterize and run FRAGSTATS to quantify the structure of the simulated landscapes. RMLands parameterization generally involves extensive research and expert team meetings, and can take weeks to years to complete. To illustrate this example we ran a 2,000 year (200 10-year timestep) simulation. We selected a broad range of class- and landscape-level metrics, including both structural and functional metrics, to assess landscape structure produced by the simulation.

TABLE 1 | Percentage of the Prospect Creek Basin case study landscape in each of the major cover types.

Cover type	%Land
Mesic-wet spruce-fir forest and woodland	25.65
Mixed conifer forest-ponderosa pine-douglas fir	33.52
Western Hemlock-Western Red-cedar forest	11.27
Mixed conifer forest-grand fir	17.80
Riparian	4.65
Mixed conifer forest-larch	3.27
Total	**96.16**

Step 4. Examine the Model Equilibration

The next step is to examine the model equilibration. We must first characterize HRV under dynamic equilibrium conditions in which the landscape fluctuates within a stable range of variation. Because the current landscape may not be operating within its HRV, it is usually necessary to allow the simulated landscape to "return" to its stable SRV. Consequently, there is usually an "equilibration period" at the beginning of the simulation during which the landscape adjusts to equilibrium conditions. Here, we will examine the magnitude and duration of the model equilibration. There is no simple way to quantify the existence and length of the equilibration period, so it is usually determined subjectively by examining the simulated trajectory of landscape change. There are several possible descriptive statistics that could be evaluated to assess the equilibration period. For pragmatic reasons, here we will consider only two.

Seral-Stage Distribution

In this section we consider the dynamics in the seral-stage distribution for each cover type. We first examine the cover-condition dynamics plots for evidence of a model equilibration period—a period at the beginning of the simulation during which the seral stage distribution is noticeably different from the remainder of the simulation. Note, it would be prudent to pay attention to only those cover types with substantial area in the simulation landscape (**Table 1**), since the dynamics for the poorly represented cover types can be unreliable or uninformative.

There is a distinct model equilibration period in landscape composition that is evident in all cover types, as illustrated in the example below in the seral-stage distribution of mixed conifer forest-ponderosa pine-Douglas fir cover type (**Figure 4**). Based on the majority of metrics, the equilibration period is roughly 200 years, but a few metrics don't equilibrate until after 500 years.

There is considerable variation in the equilibration period among cover types, as illustrated by the differences between mesic-wet spruce-fir forest and woodland (MW_SF,

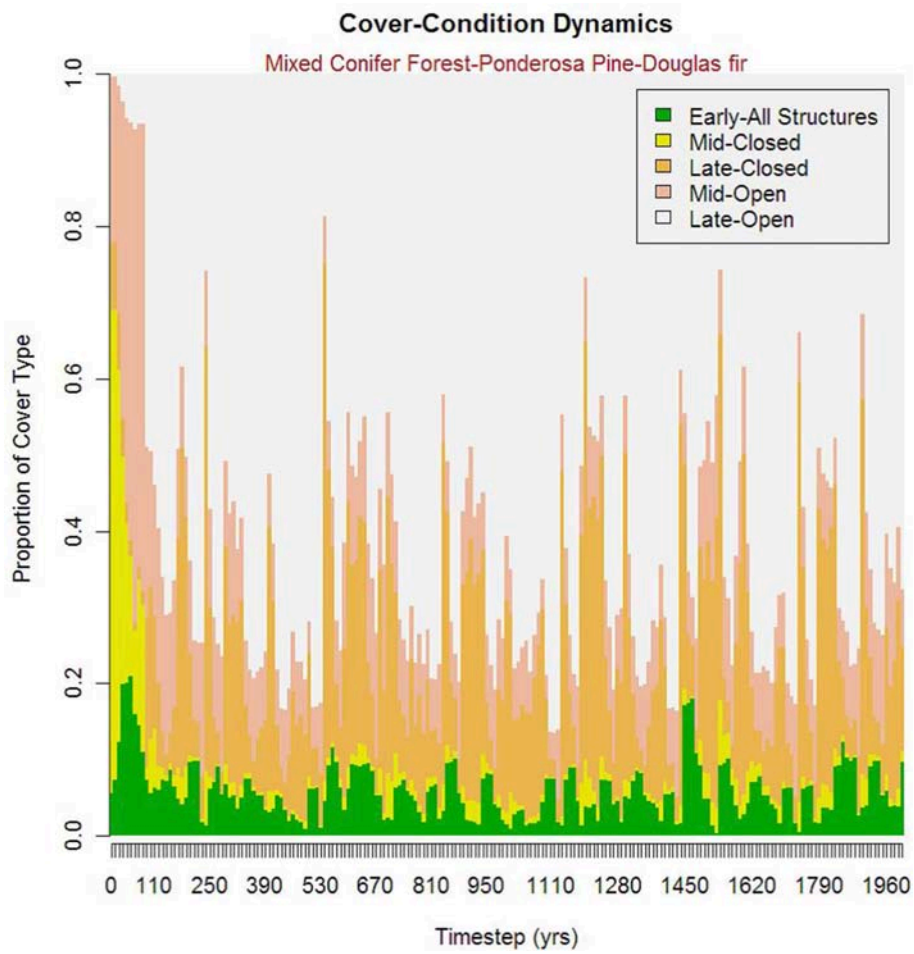

FIGURE 4 | Temporal plot of proportion of the Prospect Creek landscape covered by each of the different seral stages for one focal vegetation cover type, Mixed Conifer Forest - Ponderosa Pine-Douglas Fir.

Figure 5) and mixed conifer forest-ponderosa pine-Douglas fir (MCF_PPDF). In general, the equilibration period is relatively short, in the range of 100–150 years, for the ponderosa pine type, but considerably longer, up to 500 years, for the spruce-fire type. The differences between these cover types are likely due to dramatic differences in their characteristic disturbance regimes. The ponderosa pine type is subject to very frequent wildfires (mean fire return interval of roughly 25 years), while the spruce-fir type is subject to infrequent disturbances (mean fire return interval of roughly 200 years). The frequent disturbances in the ponderosa pine type allows the system to equilibrate rather quickly in contrast to the slow dynamic of the spruce-fir type.

Landscape Structure

The next step is to consider the dynamics in landscape structure based on the FRAGSTATS landscape-level metrics. First, we determine if there is a detectable model equilibration period in landscape structure based on the FRAGSTATS landscape-level metrics and estimate what that period is. We evaluate how this equilibration period differs among landscape metrics and identify the aspects of landscape structure that appear to be most in need of model equilibration.

There is a distinct model equilibration period in landscape structure, but it is highly variable among landscape metrics. Some metrics show a distinct model equilibration period, while others exhibit essentially no model equilibration. This indicates that some aspects of the current landscape structure are within the simulated range of variability, while others are not. In particular, the landscape metrics associated with the large patch structure (e.g., GYRATE_AM, LPI, CONTAG, **Figures 6A–C**), specifically the size and extensiveness of the large patches, are most in need of model equilibration. That is to say, the large patch structure in the current landscape departs the most from the SRV. In addition, the interspersion and juxtaposition index and Shannon's and Simpson's landscape diversity indices all exhibit a distinct model equilibration, indicating that the diversity of the current landscape also deviates considerably from the SRV. This result is consistent with the findings from the cover-condition statistics that indicate that most cover types have a current

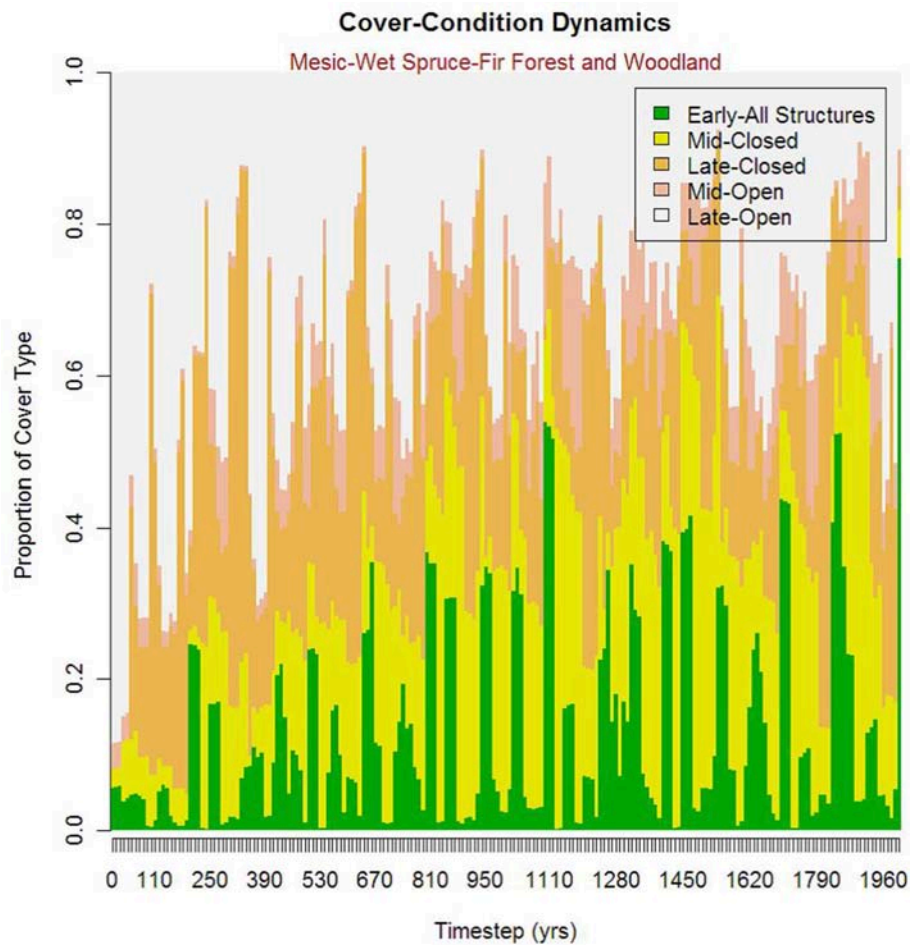

FIGURE 5 | Temporal plot of proportion of the Prospect Creek landscape covered by each of the different seral stages of one focal vegetation cover type, Mesic-Wet Spruce-Fir Forest and Woodland.

seral-stage distribution that deviate from their SRV. In contrast, many aspects of landscape structure, in particular edge density and edge contrast, do not require any model equilibration and are thus currently within their SRV. In general, with the exception of SHAPE_AM, the landscape metrics requiring equilibration do so rather quickly, mostly within 100 years.

Step 5. Evaluate the Simulated Range of Variability in Landscape Structure and Current Departure for Individual Metrics

Seral-Stage Distribution

A tabular summary of SRV in cover-condition (i.e., cover type seral-stage distribution) provides a simple means to evaluate the departure of the current condition from SRV. Given the large number of covercondition classes in this analysis, here we present only a subset of a few cover types of particular interest for this analysis. These include mixed-conifer, ponderosa pine-Douglas fir, early seral (MCF_PPDF_e), mixed-conifer forest, ponderosa pine-Douglas fir, late seral open canopy (MCF_PPDF_lo), and mesic-wet spruce-fir, late seral open canopy (MW_SF_lo). **Table 2** provides a summary of the simulated range of variability in the distribution of area among condition classes (i.e., seral stages) for these cover types and the departure of the current landscape from the simulated range of variability for each condition class, the current value of the metric, and a summary of the computed *cover type departure index* (CDI). This index represents the overall departure of a cover type from the simulated range of variability in the distribution of area among condition classes. The table also includes how many standard errors the current condition is from the mean of the simulated distribution (stderr), and the percentile the current condition is of the range of the simulated distribution (pct_srv).

We can use the information in these tables to evaluate the range of variability and departure of the current landscape composition from the SRV for the three covercondition classes listed above. We choose to quantify the SRV (HRV) based on the 5th and 95th percentiles of the simulated distribution in the percentage of the cover type comprised of each seral stage. The 5th−95th percentiles capture almost the full range of variability without being overly sensitive to extremes. Based on this we see, for example, the SRV for PLAND of MCF_PPDF_e is from 0.5 to

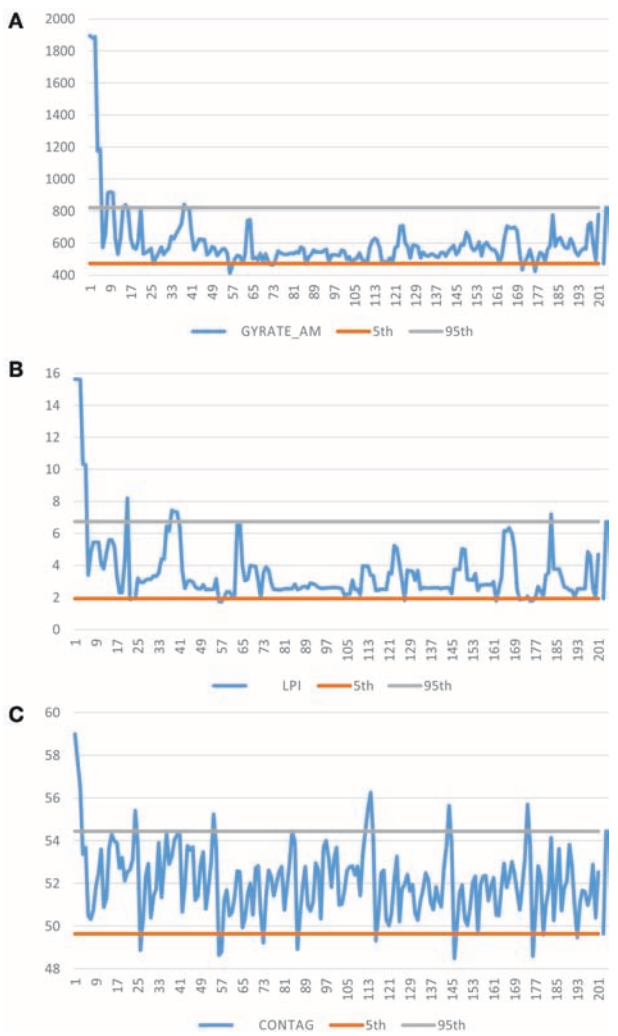

FIGURE 6 | Temporal plot of three landscape metrics within the Prospect Creek landscape. **(A)** Correlation Length (Gyrate_AM), **(B)** Largest Patch Index (LPI), **(C)** Contagion (CONTAG). The blue line represents the value of the landscape metric over the simulation time. The gray line is the upper 95th percentile of the simulated range, and the orange line is the lower 5th percentile of the simulated range.

3.4% and the median value of the SRV is 1.8%. Similarly the SRV for PLAND of MCF_PPDF_lo is 13.7 to 27.8% and the median is 23.7%. Finally, for MW_SF_lo the SRV of PLAND is 3.2 to 16.8% with a median of 8.3%. There is not sufficient space in this paper to discuss or elaborate on the SRV results for all the classes or all the metrics, but one could compute and compare SRV, current value and departure for all metrics for all covercondition classes to identify the attributes that are most departed from SRV and in what way they are perturbed from the range expected.

Table 2 also contains several measures of the current departure from the range of variability (SRV) for the amount of the landscape in each cover-condition class. There are many ways we could represent the degree of departure. This table shows three: (1) cover type departure index (CDI), ranging from 0 (no departure) to maximum (current value as a proportion of the range between median-95% confidence limit), (2) standard errors of current from distribution of SRV, (3) percentile of SRV. Focusing again on the PLAND metric for the three coverconditoin classes, we see that for MCF_PPDF_e we have a DPI of 0.1 indicating that the current value is larger than the median by 10% of the range between the median and 95th percentile. This indicates the value is well within the SRV. Different measures of the same thing are given by stderr and pct_srv, which show, respectively, that the current PLAND for this covercondition class is 1.5 standard errors above the mean of the simulated distribution and that the current value is 50th percentile of the SRV. Conversely, for MCF_PPDF_lo we see the CDI value is −2.3, indicating that the current value is lower than the median by 2.3 times (230%) the range from the median to the 5th percentile. The stderr and pct_SRV also show strong departure, with values of −66.3 and 0, respectively, indicating that PLAND of MCF_PPDF_lo in the current landscape is much lower than the range expected by the SRV. Likewise, for MW_SF_lo the current PLAND of 22.7% has a departure index (CDI) of 1.7, a stderr of 51.4 and pct_SRV of 1.0, indicating that the current extent (PLAND) of late open spruce fir is much greater than the range of the SRV.

Landscape Structure

In addition to range of variation and departure of amounts and configuration of each covercondition class, we are often interested in examining SRV in landscape structure and current departure based on the FRAGSTATS landscape-level metrics. The structure of **Table 3** is very similar to that of the covcond table above, the only difference being that instead of unique cover-condition classes (rows), we have landscape metrics which measure the composition and configuration of the entire landscape mosaic of multiple covercondition classes simultaneously. The *landscape departure index* (LDI) is computed in the same manner as the *cover type departure index* (CDI) and represents the average departure among landscape metrics from the SRV. Likewise, the standard errors from the mean of the SRV distribution and percentile of the SRV distribution are calculated the same way as well.

We can use the information in **Table 3** to identify what aspects of landscape structure exhibit the greatest SRV (not departure). Specifically, the large patch structure, specifically the size and extensiveness of the large patches and overall clumpiness of the landscape (AREA_AM, GYRATE_AM, CONTAG), exhibits the greatest SRV. Essentially, under natural dynamic conditions the coarse patch structure of the landscape fluctuates dramatically in response to coarse scale disturbances followed by succession. Large, contiguous patches of, for example, mature high-elevation spruce-fir forest are occasionally broken up by infrequent large disturbance events, generally a wildfire or mountain pine beetle outbreak, only to be followed by long periods of succession during which disturbance patches succeed and eventually coalesce to form large extensive patches again.

Table 3 also contains several measures of the current departure from the range of variability (SRV) for structure and composition of the covercondition class mosaic. For example, the

TABLE 2 | Simlulated range of variability of 12 class-level landscape metrics.

MCF_PPDF_e	95th	5th	50th	current	CDI	stderr	pct_srv
PLAND	3.4	0.5	1.8	1.9	0.1	1.5	0.5
ED	9.4	1.5	5.1	12.2	1.7	39.2	1.0
AREA_AM	267.7	15.6	57.9	4.3	−1.3	−10.3	0.0
GYRATE_AM	748.1	167.4	355.3	96.0	−1.4	−20.6	0.0
SHAPE_AM	4.4	2.0	2.9	2.1	−0.9	−15.1	0.1
CPLAND	3.4	0.5	1.8	1.9	0.1	1.3	0.5
CAI_AM	99.9	97.7	99.3	98.0	−0.8	−25.5	0.1
CWED	3.0	0.5	1.7	3.0	0.9	20.7	0.9
TECI	36.0	31.8	34.0	24.3	−4.4	−101.1	0.0
CLUMPY	0.9	0.7	0.8	0.5	−2.0	−64.4	0.0
IJI	67.7	50.3	59.8	35.9	−2.5	−64.1	0.0
AI	86.6	65.4	79.2	52.4	−1.9	−62.5	0.0
MCF_PPDF_lo	**95th**	**5th**	**50th**	**current**	**departure**	**stderr**	**pct_SRV**
PLAND	27.8	13.7	23.7	0.2	−2.3	−66.3	0.0
ED	48.5	21.8	42.0	2.0	−2.0	−66.2	0.0
AREA_AM	440.8	181.8	344.0	0.4	−2.1	−56.0	0.0
GYRATE_AM	1046.3	602.0	888.6	26.9	−3.0	−80.0	0.0
SHAPE_AM	5.3	3.9	4.7	1.2	−4.3	−104.7	0.0
CPLAND	19.4	9.9	15.9	0.0	−2.7	−64.0	0.0
CAI_AM	76.1	62.5	69.3	3.8	−9.7	−141.9	0.0
CWED	13.9	5.8	11.6	0.3	−2.0	−59.2	0.0
TECI	30.7	22.9	27.7	14.7	−2.7	−72.9	0.0
CLUMPY	0.9	0.8	0.8	0.2	−15.1	−191.7	0.0
IJI	75.0	63.7	71.0	40.3	−4.2	−98.5	0.0
AI	88.7	83.2	87.1	17.6	−17.7	−203.8	0.0
MW_SF_lo	**95th**	**5th**	**50th**	**current**	**departure**	**stderr**	**pct_SRV**
PLAND	16.8	3.2	8.3	22.7	1.7	51.4	1.0
ED	31.6	12.2	22.4	24.8	0.3	6.0	0.7
AREA_AM	1684.3	31.6	315.3	5792.4	4.0	156.5	1.0
GYRATE_AM	2308.6	233.0	808.2	7094.1	4.2	139.1	1.0
SHAPE_AM	14.2	3.6	6.9	18.0	1.5	50.8	1.0
CPLAND	14.4	2.0	6.2	17.9	1.4	47.1	1.0
CAI_AM	84.7	56.0	75.8	78.5	0.3	4.0	0.7
CWED	5.3	2.2	3.6	6.9	1.9	52.0	1.0
TECI	18.7	13.9	15.7	26.4	3.5	91.2	1.0
CLUMPY	0.8	0.6	0.8	0.9	1.8	22.9	1.0
IJI	46.3	28.3	41.2	59.4	3.6	43.5	1.0
AI	86.6	64.4	79.6	91.6	1.7	23.5	1.0

PLAND, Percentage of the landscape; ED, Edge Density; AREA_AM, Area_Weighted Mean Patch Size; GYRATE_AM, Correlation Length; SHAPE_AM, Area-Weighted Mean Shape Index; CPLAND, Core Area Percentage of Landscape; CAI_AM, Area-Weighted Core Area Index; CWED, Contrast Weighted Edge Density; TECI, Total Edge Contrast Index; CLUMPY, Clumpy Index; IJI, Interspersion and Juxtaposition Index; AI, Aggregation Index. For three covercondition classes (Mixed Conifer Ponderosa Pine Douglas Fir Early Seral (MCF_PPDF_e), (Mixed Conifer Ponderosa Pine Douglas Fir Late Seral Open Canopy (MCF_PPDF_lo), Mesic-wet Spruce Fir Late Seral Open Canopy (MW_SF_lo). For each metric, for each covercondition class we report seven statistics: (1) 95th percentile of the SRV (95th), (2) 5th percentile of the SRV (5th), (3) 50th percentile, or median, of the SRV (50th), (4) current value of the metric at beginning of the simulation (current), (5) class-level departure index (CDI), which is the value of the current condition as a proportion of the range between the 50th and 5th or 95th percentile, (6) the number of standard errors the current condition is from the mean of the simulated distribution (stderr), and (7) the current condition as a percentile of the SRV (pct_srv).

landscape departure index (LDI), ranging from 0 (no departure) to maximum (current value as a proportion of the range between median-95% confidence limit) shows that the current landscape structure departs greatly from the SRV for 8 metrics, listed here in order of decreasing departure: GYRATE_AM, AREA_AM, IJI, LPI, CONTAG, SHIDI, SHAPE_AM, SIDI. The sign of these LDI scores indicates that the current landscape is much more aggregated (CONTAG, IJI), with large and more extensive patches (AREA_AM, GYRATE_AM, LPI), which are much more complex in shape (SHAPE_AM) that would be expected under the SRV. In contrast, several other metrics are not departed from the SRV, including ED, CWED, TECI, which indicates that the amount of total edge and edge contrast in the landscape is within the SRV. Standard errors of current from distribution of SRV and percentile of SRV echo the LDI in terms of the relative departure of the different metrics.

TABLE 3 | Simlulated range of variability of 16 landscape-level metrics.

	95th	5th	50th	current	LDI	stderr	PCT_SRV
LPI	1.292809	−0.78302	−0.36629	5.812824	3.724378	137.7747	1
ED	1.55674	−1.62435	0.012545	−0.47298	−0.31442	−6.97831	0.316062
AREA_AM	0.915318	−0.55719	−0.27197	6.711543	5.881918	220.2471	1
GYRATE_AM	0.915977	−0.6705	−0.25718	6.741833	5.965976	209.386	1
SHAPE_AM	1.27749	−0.83172	−0.35159	4.137876	2.755835	81.32819	1
TCA	1.980695	−1.45541	−0.0771	0.650122	0.353399	10.03254	0.761658
CAI_AM	1.980686	−1.45542	−0.07712	0.65014	0.353416	10.03309	0.761658
CWED	1.516198	−1.65653	−0.04656	−1.05277	−0.64386	−13.8009	0.202073
TECI	1.895774	−1.36278	−0.21861	−0.75141	−0.25199	−7.28902	0.233161
CONTAG	1.357931	−1.54328	−0.0908	4.251333	2.997199	66.11022	1
IJI	1.503616	−1.32438	0.122581	−5.51436	−4.08168	−90.5089	0
SHDI	1.625125	−1.39075	0.112796	−4.21371	−2.86082	−65.4413	0
SIDI	1.659579	−1.59001	0.099262	−2.93827	−1.94674	−43.2698	0
AI	1.623673	−1.56193	−0.0149	0.396397	0.25101	5.913172	0.637306

LPI, Largest Patch Index; ED, Edge Density; AREA_AM, Area_weighted Mean Patch Size; GYRATE_AM, Correlation Length; SHAPE_AM, Area-Weighted Mean Shape Index; TCA, Total Core Area; CAI_AM, Area-Weighted Core Area Index; CWED, Contrast Weighted Edge Density; TECI, Total Edge Contrast Index; CONTAG, Contagion Index; IJI, Interspersion and Juxtaposition Index; SHDI, Shannon Diversity Index; SIDI, Simpson Diversity Index; AI, Aggregation Index. For the full mosaic of all covercondition classes taken together. Ee report seven statistics: (1) 95th percentile of the SRV (95th), (2) 5th percentile of the SRV (5th), (3) 50th percentile, or median, of the SRV (50th), (4) current value of the metric at beginning of the simulation (current), (5) class-level departure index (CDI), which is the value of the current condition as a proportion of the range between the 50th and 5th or 95th percentile, (6) the number of standard errors the current condition is from the mean of the simulated distribution (stderr), and (7) the current condition as a percentile of the SRV (pct_srv).

Conducting this evaluation shows that current departure is very sensitive to the choice of metric. For example, the cover type departure indices derived from the seral-stage distribution data (covcond) vary greatly for the cover types with significant area in the Prospect Creek landscape. Similarly, the landscape departure indices based on individual landscape structure metrics range similarly widely. For example, the aggregation index (AI) at the landscape level has a departure index of 0.23, indicating the current condition is well within the range of the SRV. In contrast, correlation length (GYRATE_AM) at the landscape level has a departure index of 5.97 because the current landscape condition is exceeds the 95th percentile of the SRV by 5.97 times the range from the median to the 95th percentile. Thus, the choice of metric can lead to opposite conclusions regarding the departure of the current landscape. For this reason, a multivariate approach is necessary, whereby several metrics are evaluated together.

MULTIVARIATE TRAJECTORY ANALYSIS

Landscape-Level Landscape Multivariate Trajectory Analysis

We implemented a landscape trajectory analysis (sensu Cushman and McGarigal, 2007) with multi-temporal principal components analysis (e.g., Cushman and Wallin, 2000) to show the main pattern among landscape-level metrics (e.g., FRAGSTATS; McGarigal et al., 2012) across the 200 time steps of the simulation (**Figure 7**). The PCA was done on a table of centered and standardized values of 14 landscape-level metrics: ED, edge density; CWED, contrast-weighted edge density; TECI, total edge contrast index; SHDI, Shannon diversity index; IJI—interspersion and juxtaposition index; SIDI, Simpson diversity index; AI, aggregation index; TCA, total core area; CAI_AM, area-weighted core area index; CONTAG, contagion; GYRATE_AM, area-weighted mean patch radius of gyration; LPI, largest patch index; AREA_AM, area-weighted mean patch size; SHAPE_AM, area-weighted mean patch shape index.

The first two axes explain 70% of the total variance in class-level landscape structure, with the first axis explaining 43% and the second 37%. The first axis is highly aligned with CONTAG, IJI and SHDI. CONTAG increases to the left, and IJI and SHDI increase to the right, indicating that the right represents a more heterogeneous condition with lower aggregation, higher diversity of patches and higher interspersion of patches, while the left indicates conditions where there is high homogeneity and aggregation of the landscape. The second axis is associated with patch interspersion, and edge contrast, with highest patch interspersion and edge contrast to the top of the axis. The black ellipse on the plot indicates the 95$^{\%}$ probability ellipse for all points in the plot. The red vectors point in the direction of increasing value of each metric. For example the upper right quadrant of the PCA is areas with high edge density, low core area, low aggregation, and high edge contrast. The lower left quadrant is the opposite: conditions characterized by high landscape aggregation, high core area, low edge density and low edge contrast. The upper left quadrant is represented by extreme conditions associated with very high largest patch size, very high area-weighted mean patch size, and very high area-weighted mean patch radius of gyration. This represents conditions with very large and very extensive patches.

The numbers on the graph represent the time step in the simulation. The location of the time steps across the PCA space shows the trajectory of change in multi-variate landscape structure from the current (initial) condition (0) to the end of the simulation (200). The current condition is far to the upper left, indicating that the current landscape has much larger, more

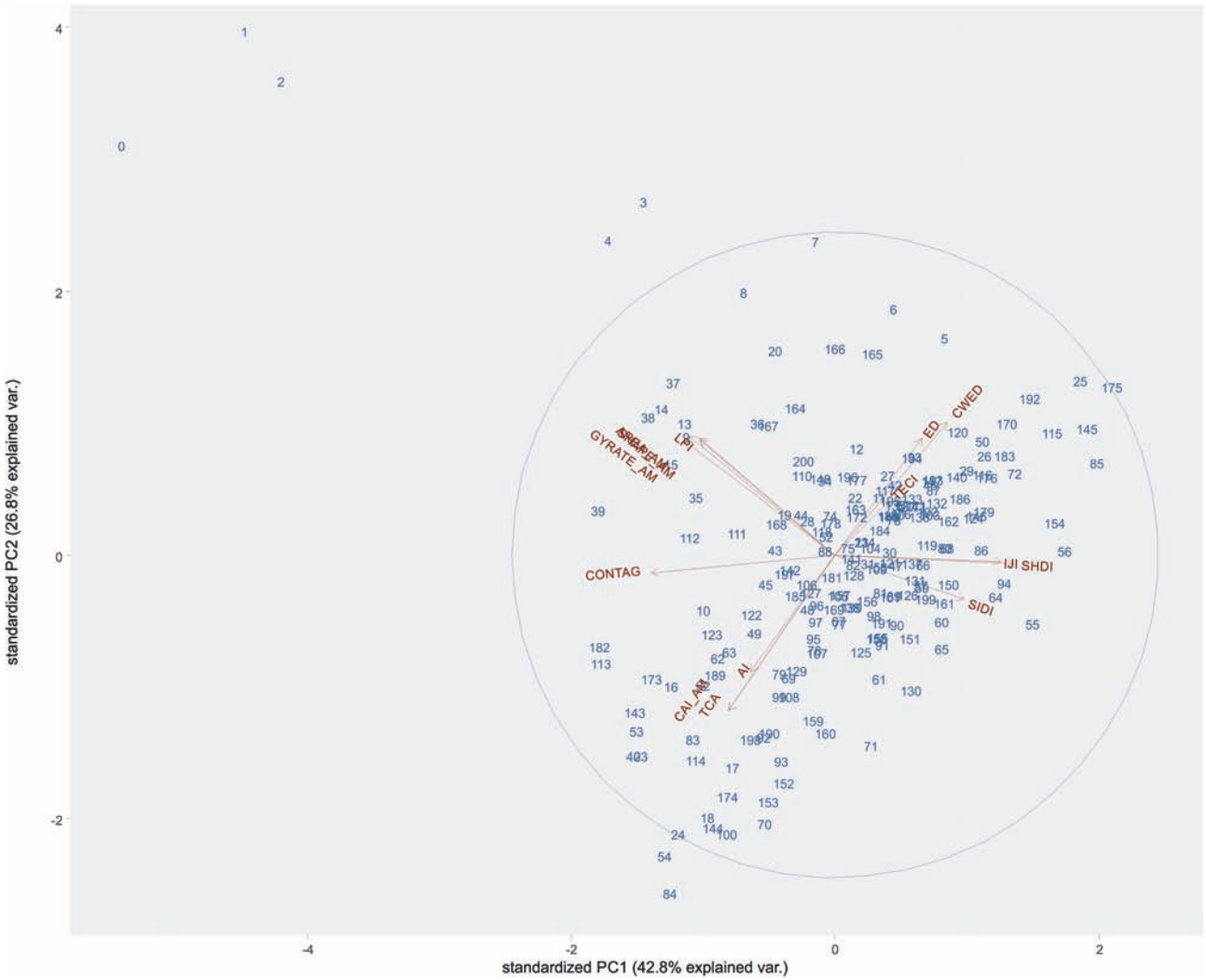

FIGURE 7 | Multi-temporal principal components plot of landscape-level metrics in the Prospect Creek watershed across the simulation time. Blue numbers represent landscape conditions at each time step, which represent years of simulation/10. The blue ellipse contains 95% of the simulated range in principal components space. The red vectors represent the direction of change in each of the landscape metrics, whose acronyms are shown at the end of each vector. AI, Aggregation Index; TCA, Total Core Area; CAI_AM, Area-weighted Core Area Index; CONTAG, Contagion; GYRATE_AM, Correlation Length; AREA_AM, Area-weighted Mean Patch Size; LPI, Largest Patch Index; ED, Edge Density; CWED, Contrast-weighted Edge Density; IJI, Interspersion and Juxtaposition Index; TECI, Total Edge Contrast Index; SHDI, Shannon's Diversity Index; SIDI, Simpson's Diversity Index.

extensive, and more connected patches than expected under the SRV. The distance from the initial condition (0) to the centroid of the PCA (which is 7.4 PCA axis units in this case) is a measure of departure from the center of the SRV, and the distance from the boundary of the 95% ellipse (4.9 in this case) is a measure of the departure from the SRV range. The ratio of these, 8.4/4.9, or 1.71, indicates how far the current value is beyond the SRV ellipse in terms of the width of the SRV ellipse. This means that the current multivariate LDI index is 1.71, given that the current condition is 1.71 times farther from the centroid of the PCA than the full width of the SRV condition.

During the simulation, the landscape condition returns to within the SRV (95% ellipse) within 5 time steps (50 years). There is considerable dynamic variation in landscape structure over the simulation time, with some quasi-periodic fluctuation between upper right (high edge density and low core and contagion) and lower left (low edge density and high core and contagion). However, never in the simulation time does the condition of the landscape approach anything like the initial (current) condition, which is characterized by very large, highly connected and extensive patches with low diversity. The current condition is far outside the SRV, but the patterns change relatively quickly over the simulation time to return to within the 95% ellipse, showing relatively rapid recovery once the historic disturbance regime is reestablished.

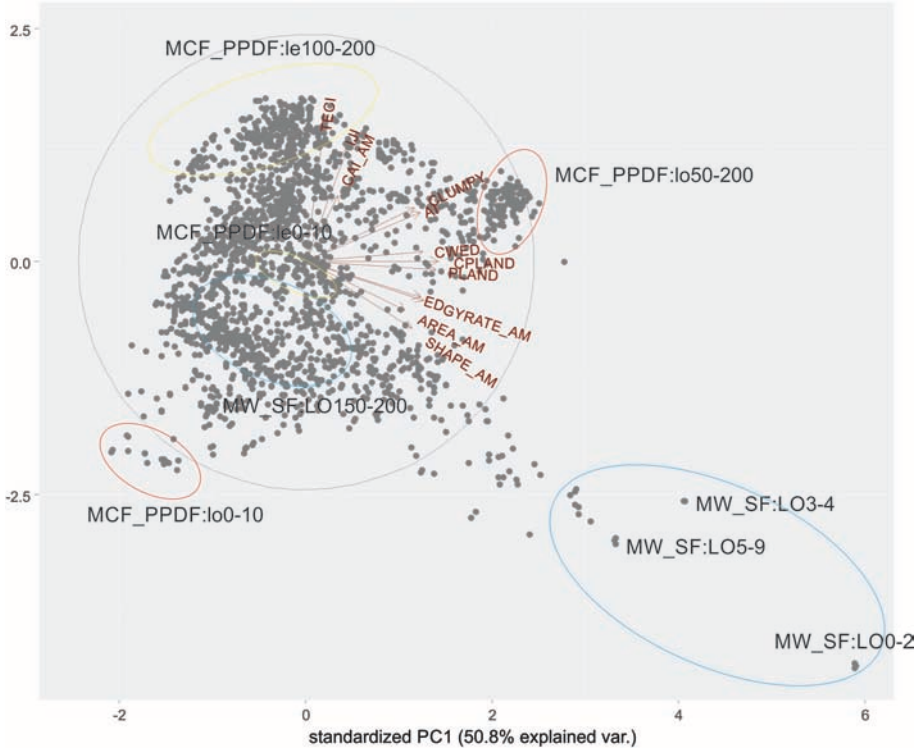

FIGURE 8 | Multi-temporal principal components analysis of class-level metrics in the Prospect Creek watershed across the simulation time. Gray dots are combinations of cover type at a given seral stage at a given simulation time step. The gray ellipse contains 95% of the simulated range in landscape structure space. The red vectors represent the direction of increase of each landscape metric and metric acronyms are labeled at the end of each vector. The blue ellipses show cover-seral conditions for two cover types (Mixed-Conifer Ponderosa Pine-Douglas Fir Late Seral Open Canopy - NCF_PPDF; Mesic-Wet Spruce-Fir Late Seral Open Canopy - MW_SF) at early and late simulation times. Simulation times are indicated by the numbers at the end of the acronym. For example, MCF_PPDF:lo0-10 ellipse encloses the initial condition and first ten time steps of the Mixed-Conifer Ponderosa-Pine Douglas Fir Late Seral Open Canopy cover-seral class in landscape structure space. TECI, Total Edge Contrast Index; IJI, Interspersion and Juxtaposition Index; CAI_AM, Area-weighted Core Area Index; CLUMPY, Clumpy Index; AI, Aggregation Index; CWED, Contrast Weighted Edge Density; CPLAND, Core Area Percentage of the Landscape; PLAND, Class Percentage of the Landscape; ED, Edge Density; GYRATE_AM, Correlation Length; AREA_AM, Area-weighted Mean Patch Size; SHAPE_AM, Area-weighted Shape Index.

Class-Level Landscape Multivariate Trajectory Analysis

We again used multi-temporal principal components analysis (e.g., Cushman and Wallin, 2000) to show the main pattern among cover-condition classes across the 200 time steps of the simulation (**Figure 8**). The PCA was done on a table of centered and standardized values of 12 class-level metrics: TECI, total edge contrast index; IJI, interspersion and juxtaposition index; CAI-AM, area-weighted core area index; CLUMPY, clumpy index; AI, aggregation index; CWED, contrast-weighted edge density; CPLAND, core area percentage of the landscape; PLAND, percentage of the landscape; ED, edge density; GYRATE_AM, area-weighted mean radius of gyration; AREA_AM, area weighted mean patch size; SHAPE_AM, area-weighted shape index. The first two axes explain 85% of the total variance in class-level landscape structure, with the first axis explaining 51% and the second 34%. The first axis is highly aligned with PLAND and CPLAND, with these metrics increasing to the right. This axis is associated with very extensive cover types to the right and low extent of the cover types to the left. The second axis is highly associated with patch interspersion, and edge contrast, with highest patch interspersion and edge contrast to the top of the axis. The black ellipse on the plot indicates the 95% probability ellipse for all points in the plot. The red vectors point in the direction of increasing value of each metric.

The points on the graph indicate the locations of each cover type at each time-step in the landscape structure space. To illustrate the temporal change in landscape structure in a few key landcover types we have located and labeled the initial and ending locations of four cover-condition classes: MW_SFlo—mesic-wet, spruce-fir, late seral, open canopy; MCF_PPDF:lo—mixed conifer forest, ponderosa pine, Douglas fir, late seral, open canopy; MCF_PPDF:e—mixed conifer, ponderosa pine, Douglas fir, early seral. The change in conditions over the simulation time is illustrated by the movement of the points for that cover-condition class across these two-dimenions of the PCA. For example, MW_SF:Lo (blue ellipses) starts far to the right of axis 1 and bottom of axis 2, with conditions characterized by very

high extent (percent of the landscape) and very large patch size (AREA_AM, GYRATE_AM). This indicates that at the beginning of the simulation (current condition), the landscape is highly dominated by large, complexly shaped patches of mesic-wet late seral open canopy spruce fir. This structure is far outside the 95% ellipse of the simulated range (SRV), indicating the current condition of the landscape departs substantially from expected under the historic disturbance regime. At the end of the simulation time (which represents the simulated range of conditions under the historic disturbance regime), this cover-condition class has moved toward the left of axis 1 and somewhat below the center on axis 2. This indicates that under the simulated historical disturbance regime mesic-wet spruce fir late seral open canopy class would likely exist in relatively moderate extent, with much smaller and simpler shaped patches than in the current condition.

In contrast to MW_SF:Lo, which our simulation predicts is more extensive than expected under the SRV, MCF_PPDF:Lo shows the opposite response. Specifically, at the beginning of the simulation mixed conifer ponderosa pine, Douglas fir, late seral open canopy is the farthest to the left on axis 1 of any cover-condition class, indicating very low extent and small patches. During most of the simulation, however, this cover-condition class moves far to the right on axis 1 and up on axis 2, such that under the SRV it is expected to be the most extensive cover type, with the largest and most complex shaped patches.

The same exercise could be repeated for each cover-condition class, calculating the distance in PC space (e.g., displacement, Cushman and McGarigal, 2007) from the initial condition to the centroid of the distribution of the SRV or the 95% ellipse. Making this calculation we see that MW_SF:Lo and MCF_PPDF:Lo are the two cover-condition classes that are most departed from multi-variate class-level pattern in their current condition compared to the SRV, with late-open spruce fir much more extensive and late-open ponderosa pine, Douglas fir much less extensive than expected under the SRV. Given landscape patterns are inherently multivariate, this kind of analysis using multi-temporal PCA across the full simulation time is more informative and comprehensive, although less intuitive, than looking at plots for individual metrics for individual cover-condition types. The number of time steps it takes the simulation to change the landscape structure for each cover-condition type to within the SRV, or 95% ellipse, is a measure of the amount of time needed for recovery of landscape patterns once a historical disturbance regime is re-established. From this we see it takes a different amount of time for MW_SF:Lo (∼150 years) than for MCF_PPDF:Lo (∼60 years). This shows that the departure of MW_SF:Lo from SRV is not only larger (e.g., distance in PCA space), but less responsive for recovery (time to return within the SRV).

DISCUSSION

A resilience-based management approach facilitates regional planning by providing evaluations of current ecological conditions relative to system equilibrium and reference states (Hessburg et al., 2013; McIntyre et al., 2014; Tambosi et al., 2014; Rappaport et al., 2015; Chambers et al., 2019). Importantly, operationalizing the concept of resilience into an analytical framework enables the optimization of management actions to achieve have the greatest benefits (e.g., McGarigal et al., 2018). Chambers et al. (2019) reviewed six key components of a resilience-based approach, including (1) formalizing the concept of managing for adaptive capacity, (2) selecting an appropriate spatial extent and grain, (3) understanding the factors influencing the resilience of ecosystems and landscapes, (4) the importance landscape context in measuring and defining resilience, (5) pattern and process interactions and their variability, and (6) relationships among ecological and spatial resilience and the capacity to support habitats and species. The purpose of this paper is to provide an introduction to concepts and methods from landscape ecology to implement these six components of assessing and managing for ecological resilience.

A spatially explicit approach coupling geospatial information on ecological system characteristics and disturbance provides the foundation for resilience-based management. Landscape ecology is the science of pattern-process relationships and, in particular, how patterns of disturbance, recover and ecological conditions drive ecological processes (Turner, 1989). The tools of landscape ecology, including landscape pattern analysis and landscape dynamic simulation modeling provide a means to implement the six components of the ecological resilience framework (Chambers et al., 2019). In this paper we provide a case study landscape of using landscape pattern analysis (e.g., McGarigal et al., 2012) and landscape dynamic simulation modeling (e.g., Littell et al., 2011; McGarigal et al., 2018) to assess the ecological condition of a case study landscape and how the current condition of that landscape departs from the range of conditions expected under a historic disturbance regime.

In this example (1) we formalize the concept of managing for adaptive capacity under the framework of assessing current conditions relative to the range of conditions expected under a natural disturbance regime, which can subsequently be used to optimize management scenarios to best achieve resilient landscape conditions (e.g., McGarigal et al., 2018). Our example focuses on (2) developing a meaningful and appropriate landscape definition for analysis, including decisions regarding grain, extent, thematic content and thematic resolution. This is critical, as all pattern-process relationships, including assessments of resilience, depend on correctly defining the landscape relative to the dominant ecological characteristics and the drivers that affect their value and dynamics (Wu, 2004; Buyantuev and Wu, 2007). We assess (3) factors affecting the resilience of ecosystems and landscapes in this case study by focusing on the processes of how natural disturbance regimes interact with topography, climate and vegetation to driver patterns of ecosystem structure (Romme and Knight, 1981). The use of a spatially explicit, dynamic landscape simulation model (Mladenoff and Baker, 1999; Costanza and Voinov, 2004) allows (4) assessment of the landscape context in evaluating resilience.

Specifically, in this case our simulation of the expected range of ecological conditions under a natural disturbance regime provides a framework for evaluating the current condition relative to the range of conditions the system would exist in without human perturbation. This provides the key reference framework for evaluating current conditions relative to measures of ecological resilience, including degree of departure from reference conditions (simulated range of natural variation), and ability of the system to recover (how rapidly it reenters the range of simulated range of variability once a natural disturbance regime is reestablished. This framework is formally based on (5) evaluating pattern-process interactions (Turner, 1989) and their variability, which is a key component of defining, measuring and managing for ecological resilience. Finally, (6) the assessment we provide can be linked to assessing the relationship between landscape patterns and particular ecological processes, such as maintenance of habitats and species (e.g., Cushman et al., 2011). For example, Cushman and McGarigal (2007) used the RMLands model to simulate several alternative forest management scenarios and coupled them to multi-scale habitat relationships modeling for a focal species (American marten, *Martes americana*) and used multivariate landscape trajectory analysis to quantify the relative impacts of different forest harvest regimes on the extent, pattern and trajectory of change of habitat for this forest dependent species. Similarly, Cushman et al. (2011) used RMLands and multi-scale habitat modeling to project the effects of climate change, forest restoration treatments and fire suppression on habitat extent and pattern of two focal species (American marten and flammulated owl) in the Prospect Creek case study landscape. That analysis showed that forest restoration treatments, at levels realistic given management and logistical constraints, are unlikely to greatly affect wildfire disturbance regimes and that climate driven changes in fire regimes likely will decrease habitat quality for the closed-forest dependent American marten, but are less likely to severely affect habitat quality for the open-canopy specialist flammulated owl.

The case study example in this paper focuses on a particular watershed in the U.S. Northern Rocky Mountains and measures how the current landscape composition and configuration differ from the expected range under a natural disturbance regime. The example is intended to be heuristic and illustrative of the ideas, methods and tools used by landscape ecologists to assess current conditions relative to reference conditions. In this case we defined the landscape based on a patch mosaic model with cover types defined by combinations of dominant vegetation type, stand age and canopy closure. This choice of landscape definition fundamentally affects all analyses, results and interpretation. We do not propose that this particular landscape definition is ideal for all, or even any, particular applications. We chose since it is intuitively familiar to most managers and scientists, and since many tools we utilize employ a patch mosaic framework (e.g., FRAGSTATS, McGarigal et al., 2012, RMLANDS, McGarigal et al., 2018), and because many past assessments of landscape effects on ecological processes have used similar landscape definitions (e.g., Cushman and McGarigal, 2007; Cushman et al., 2011; McGarigal et al., 2018).

We illustrate the use of landscape pattern analysis with FRAGSTATS (McGarigal et al., 2012) as a means to quantitatively measure the spatial attributes of landscapes over time and across space. The ability to comprehensively and quantitatively evaluate and compare ecological conditions across space and time is essential to measure the characteristics of current conditions and compare them to reference frameworks of other landscapes or dynamic ranges under historic disturbance regimes (e.g., McGarigal et al., 2018), or to outcomes of simulated alternative future scenarios (e.g., Kaszta et al., 2019). Landscape pattern analysis is a foundational idea in landscape ecology and is a powerful tool to measure and evaluate ecological conditions in the context of ecological resilience. In our example we illustrated this by using FRAGSTATS to measure a number of spatial attributes of the case study landscape, which collectively quantified many attributes of its composition and configuration which we chose based on their utility in describing major gradients of landscape structure (e.g., Cushman et al., 2008), and their known associations with many ecological processes (e.g., Grand et al., 2004; Chambers et al., 2016).

We used spatially-explicit dynamic landscape simulation modeling with RMLANDS to provide a spatio-temporal reference framework for assessing some aspects of ecological resiliency. Landscape dynamic simulation modeling is extremely useful to project the dynamic range of conditions one would expect under different scenarios of disturbance, succession, management and climate. A reference framework to compare current conditions against quantitatively is an essential foundation for any rigorous assessment of resilience. Reference frameworks can be constructed by comparing focal landscapes to other landscapes which have particular reference characteristics (e.g., comparing managed or disturbed landscapes to those in protected areas such as Wilderness), or to the distribution of all landscapes in the study region (e.g., how does the focal landscape compare to the range of conditions more broadly). These approaches in a sense "trade space for time" by assuming that the current conditions of the reference landscapes reflect some important aspects of the past conditions of the reference landscape, relevant for assessing resilience. There are strengths and weaknesses of that approach. The strength is it is comparing real current conditions to real actual conditions in reference landscapes, which removes uncertainty arising from modeling projections. The weakness is that it is not clear how well current conditions in the reference landscape actually reflect a meaningful benchmark for assessing resilience, as they are physographically and ecological different than the focal landscape, and it is difficult to find any reference landscape that is unaffected by perturbation and human impacts.

The landscape simulation modeling approach for developing reference frameworks has a number of important advantages. First, it avoids the challenge of trying to compare ecologically and physiographically different areas, by simulating dynamic changes over time on focal landscapes themselves. Second, it removes the challenge of the legacy effects of past disturbance histories, which necessarily will differ between different current landscapes. Instead, it allows simulation of expected ranges of ecological

condition under a given set of disturbance-succession-climate-management scenarios. This provides a strong means to compare current conditions to the range of reference conditions expected under, for example, a natural disturbance regime, or to compare current conditions to what would be expected under a set of future alternative scenarios (e.g., McGarigal et al., 2018).

SCOPE AND LIMITATIONS

This example was necessarily simplified and intended as a heuristic example to fit into the format and length of a journal article. Our goal was to present the ideas, methods and tools for this kind of assessment, rather than to provide a fully realistic and completely developed example. Accordingly, we provide comparison of a single case study landscape to the reference condition of the historic disturbance regime. This allowed us to introduce landscape definition, landscape pattern analysis, landscape simulation modeling, and to use them to compare current conditions to the range expected under the historic natural disturbance regime. This enables us to measure landscape patterns and compare them to simulated ranges. By doing this we showed that the current landscape departs extensively from the range of historic conditions. We showed how we can use univariate and multivariate analyses to plot trajectories of change from current conditions to the range of simulated conditions under the natural disturbance regime. We showed how we can calculate the degree of departure from the simulated range based on FRAGSTATS metrics, and how different metrics provide different views of departure or perturbation of landscape patterns, and how multivariate methods, such as multi-temporal PCA (Cushman and Wallin, 2000) and landscape trajectory analysis (Cushman and McGarigal, 2007) provide a means to quantify the degree and nature of difference between current conditions and the simulated natural range of variation.

We used a simple example of time for the simulation to return the current condition to within the range of natural variation as a heuristic measure of one aspect of capacity for ecological recovery. This idea uses the time it would take for a reestablished natural disturbance regime to move the landscape back into the range of natural variability. As a heuristic example this has some utility to illustrate the idea, but it is not realistic for a number of reasons. For example, there are very few real landscapes where it is politically, socially or even physically possible to reestablish a natural disturbance regime as it would have existed prior to human perturbation. As such our measure of ecological ability to recovery is meant to be an abstract representation of the relative degree to which the ecosystem could recover, rather than a practical measure of how it actually could be recovered. We feel that the example given here, while, simple, serves is main purpose of describing the methods, tools, and approaches for landscape pattern analysis and landscape simulation modeling in a context relevant to assessing ecological resilience.

To implement these ideas more realistically several extensions and elaborations on our approach would be needed. An example of a recent analysis of this kind will serve to illustrate this. McGarigal et al. (2018) modeled historical range of variability and alternative management scenarios in the upper Yuba River watershed, Tahoe National Forest, California. The purpose of the project was to evaluate the degree of departure of the current landscape from historical ranges under a natural disturbance regime as a benchmark to evaluate ecological resilience, and to design and evaluate the impacts of alternative forest restoration scenarios intended to reestablish aspects of landscape structure and dynamics consistent with the historical range. McGarigal et al. (2018) simulated the dynamics in vegetation driven by wildfire during the historical reference period (ca. 1550–1850) and quantified the range of variability in composition and configuration of the landscape mosaic, and compared the results to the current landscape to quantify departure. They also created a set of eight alternative management scenarios reflecting different objectives and applying different treatment types and intensities and conducted 20 replicate 100-year simulations of each of these management scenarios and quantified the range of variability in landscape composition and configuration. Then, the range of variation in each landscape attribute among management scenarios was compared with the historical range of variability and the current landscape to determine the potential for management scenarios to move the current landscape toward its historical range of variability. McGarigal et al. (2018) found that their study landscape during the historical reference period was best characterized as a shifting mosaic of vegetation types and conditions and was subject to a high wildfire disturbance rate. Due to fire suppression and other human landscape changes, the current landscape departs from the historical range of variability in the composition and configuration of the vegetation mosaic, and more so in some attributes than others. Scenario analysis revealed the comparative effects of alternative management strategies on landscape composition and configuration. The quantitative approach used by McGarigal et al. (2018) demonstrates the feasibility of creating detailed, specific, and quantitative desired landscape conditions, and monitoring progress toward achieving those conditions. In the context of ecological resilience, it shows how landscape pattern analysis can be coupled to simulation of historic and alternative future conditions, under realistic management and restoration scenarios, to evaluate current conditions relative to the concepts of ecological resilience, including resistance to and recovery from perturbations of ecological pattern-process relationships. One important result of the scenario analysis demonstrates that active vegetation management involving a combination of mechanical and prescribed fire treatments has the potential to emulate many aspects of landscape structure that would occur under a natural disturbance regime, but it would require a much higher intensity of treatment than we are accustomed to—perhaps as much as 10 times the current treatment rate.

CONCLUSION

We illustrate how to combine landscape pattern analysis with spatially-explicit, dynamic landscape simulation modeling to evaluate the condition of a case-study landscape relative to its

expected dynamic range under a historic disturbance regime, and to use this information on departure in current conditions and ability of the landscape pattern to recover to within the range as measures of perturbation and resilience of the ecosystem, respectively. We showed the importance of carefully defining the study objective, choosing an appropriate landscape definition, and implementing realistic and relevant analyses and simulations at appropriate spatial and temporal scales. Simulation models provide means to quantify the expected range of species abundance, community structure and landscape patterns under a variety of scenarios, including the natural disturbance regime, current disturbance regime, and possible future regimes under alternative management and climate scenarios. Landscape pattern analysis and multivariate trajectory analysis then enable quantification of current conditions and change vectors relative to historic ranges of variability under natural disturbance regimes and alternative future scenarios of management, climate and natural disturbance. Together this combination of tools provides a means to define the conditions of a desired state for a healthy ecosystem and to quantify the degree of resistance and resilience of the system to perturbation, and to measure and monitor the departure from the range of natural variability in the system dynamics. Evaluating the structure and composition of landscapes relative to historical, current and future ranges of variability is fundamental to providing context and guiding management in the face of rapidly changing climate, disturbance regimes and the resulting structure and function of ecological systems (Littell et al., 2011, 2018), and their impacts on focal species (e.g., Cushman et al., 2011; Wan et al., 2019).

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article.

AUTHOR CONTRIBUTIONS

SC and KM jointly conceptualized the scope of the paper and wrote the paper. KM conducted the RMLands simulations. SC conducted the multitemporal trajectory analysis.

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Resilience Management for Conservation of Inland Recreational Fisheries

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Resilience thinking has generated much interest among scientific communities, yet most resilience concepts have not materialized into management applications. We believe that using resilience concepts to characterize systems and the social and ecological processes affecting them is a way to integrate resilience into better management decisions. This situation is exemplified by inland recreational fisheries, which represent complex socioecological systems that face unpredictable and unavoidable change. Making management decisions in the context of resilience is increasingly important given mounting environmental and anthropogenic perturbations to inland systems. Herein, we propose a framework that allows resilience concepts to be better incorporated into management by (i) recognizing how current constraints and management objectives focus on desired or undesired systems (specific fish and anglers), (ii) evaluating the state of a system in terms of how both social and ecological forces enforce or erode the desired or undesired system, (iii) identifying the resilience-stage cycles a system state may undergo, and (iv) determining the broad management strategies that may be viable given the system state and resilience stage. We use examples from inland recreational fisheries to illustrate different system state and resilience stages and synthesize several key results. Across all combinations of socioecological forces, five common types of viable management strategies emerge: (i) adopt a different management preference or focus, (ii) change stakeholder attitudes or behaviors via stakeholder outreach, (iii) engage in (sometimes extreme) biological intervention, (iv) engage in fishery intervention, and (v) adopt landscape-level management approaches focusing on achieving different systems in different waters. We then discuss the challenges and weaknesses of our approach, including specifically the cases in which there are multiple strong social forces (i.e., stakeholders holding competing objectives or values) and situations where waters are not

readily divisible, such as rivers or great lakes, and in which spatial separation of competing objectives will be difficult. We end with our vision of how we believe these types of operationalized resilience approaches could improve or transform inland recreational fisheries management.

Keywords: adaptive cycles, anglers, complex systems, fisheries management, invasive species, natural resource conservation, resilience thinking, socioecological systems

INTRODUCTION

The idea of resilience has become widely attractive, and it is recommended that governance systems "manage for resilience" (Garmestani and Allen, 2014; Cosens and Gunderson, 2018; Burnetta et al., 2019). Yet, few descriptions of practical approaches to accomplish this have been made since the inception of the idea (Grafton et al., 2019). We suspect that in many cases, a myriad of definitions and perhaps misuse of resilience concepts has delayed the ability to operationalize resilience. Resilience is also an emergent property (Gunderson, 2000) that is difficult to quantitatively measure and consequently use for management decisions (O'Brien and Leichenko, 2000; Carpenter et al., 2001; Meyer, 2016; Pimm et al., 2019). Regardless, there have been efforts to operationalize resilience concepts across diverse disciplines, such as engineering (Francis and Bekera, 2014), land use and planning (Meerow et al., 2016), psychology (Block and Block, 1980; Tugade et al., 2004), social sciences (Adger, 2000), production systems (e.g., forestry, community gardening, and aquaculture; Okvat and Zautra, 2011; Rist and Moen, 2013; Rist et al., 2014), environmental education (Krasny and Tidball, 2009; Krasny and Roth, 2010), coastal development (Adger et al., 2005; Lloyd et al., 2013), and commercial (Marshall and Marshall, 2007; Coulthard, 2012) and recreational fisheries (Arlinghaus et al., 2013; Post, 2013).

Though the term resilience is used differently across disciplines, the concept related to natural resource management was made notable by Holling (1966) and the primary concepts were then summarized by Holling (1973). This and subsequent works detailing aspects of resilience (many from the Resilience Alliance) have generally defined resilience as the magnitude of a disturbance that will trigger a shift between alternative stable states of a system. This implies that systems characterized by greater or lesser resilience will be, respectively, less or more likely to shift resilience stages or even slip into alternative system states given a similar perturbation. The concept of resilience has also been supported by development of and adaptation to complementary processes, including adaptive management (Walters, 1986) and panarchy (Gunderson and Holling, 2002). These developments have likely propelled resilience concepts beyond scientific investigation to be at least superficially embraced by diverse institutions involved in the governance of natural resources, from forestry and fisheries to coastal human communities (Benson and Garmestani, 2011; Rosati et al., 2015). This is further evidenced by management agencies proclaiming their goals of "managing for resilience," as well as by requests for proposals prompting investigation of resilience concepts. Therefore, we believe that instead of "managing for resilience," we could view resilience as a "system characteristic" that can be managed. This would provide a more meaningful and valuable framework for operationalizing resilience concepts.

The purpose of applying resilience concepts is to produce adaptable management and governance structures more capable of sustaining key system services under a range of conditions (Holling and Meffe, 1996). That is, governance structures must assess how to sustain key system services in the face of unpredictable, yet inevitable, changes, and mounting perturbations (Holling and Meffe, 1996). Such changes and perturbations appear pervasive in the current context of a deeply and rapidly changing climate (Milly et al., 2008; Paukert et al., 2016), increasing globalization (Young et al., 2006), intensifying loss of species and biodiversity (Pimm and Raven, 2000), and accelerating technological advance and consumption [(United Nations Environment Programme (UNEP) and International Union for Conservation of Nature (IUCN), 2011)]. These types of changes are likely to disproportionately affect systems with lesser resilience. Management agencies have limited resources to sustain key system services, and a resilience framework can assist with allocating these finite resources more efficiently. Yet, a looming problem exists where integration of resilience to natural resource decision making is lagging or has never begun. Resilience concepts have not been fully integrated into routine decision-making structures by management agencies in the developed world (Holling and Meffe, 1996; Berkes, 2010). They are even less recognized in the developing world, and although resilience concepts may provide opportunities to enhance socioeconomic benefit from natural resources, practical methods of incorporating these concepts into resource management are required [National Academies of Sciences, Engineering, and Medicine (NAS), 2019].

We argue that the need for operationalized resilience is strong in many disciplines, but we turn our attention to one specifically—inland recreational fisheries in which humans catch fish for the primary purpose of leisure, though this may also overlap with other purposes, such as food or income (Brownscombe et al., 2019). Recreational fisheries are complex socioecological systems that are characterized by dynamic feedbacks between fish and angler populations (Arlinghaus et al., 2007, 2013, 2017; Daedlow et al., 2011; Pope et al., 2014). Resilience ought to be particularly pertinent to these fisheries, given the stresses inland systems face from climate change, water-use demands, urbanizing human populations, and invasive species (Lynch et al., 2017; Brownscombe et al., 2019). These socioecological disturbances have already been demonstrated to

shift systems from one state to another (Arlinghaus et al., 2017). Temperature changes can alter growth and survival of fishes, which can benefit and limit certain fish populations (Sharma et al., 2007). Stocking of large piscivores can result in top-down effects, which can cascade to primary producers and either result in an increase or decrease in vegetation, depending on the number of trophic levels in the system (Eby et al., 2006). Invasive species can alter ecological communities and in turn reduce the quality of important recreational fisheries (Cucherousset and Olden, 2011). Some of these shifts were unexpected and have compromised many key system services. The multiple challenges facing recreational fisheries emphasize the importance of robust decisions in the face of an uncertain and unpredictable future.

The objective of this work is to provide a practical framework that describes how management agencies can "operationalize resilience"—that is, describe how resilience concepts can be used to frame selection of management strategies and decisions. We do not attempt to redefine core resilience concepts, but rather connect what has been established to existing management options for inland recreational fisheries. Our intention is to highlight resilience as a system characteristic to be considered when making management decisions. To accomplish this we (section Why Resilience Is Important for Management of Inland Recreational Fisheries) describe the importance and application of resilience concepts to the specific discipline, managing inland recreational fisheries for resilience, and (section Conceptual Model for Operationalizing Resilience Management of Inland Recreational Fisheries) present a conceptual model for operationalizing resilience management. We then (section Results) explore how the conceptual model may be used to identify viable management strategies. Following this we (section Discussion) discuss resilience-management linkages and address exceptional cases that may be problematic for our conceptual model. Finally, we (section Synthesis and Looking Forward) envision a future for recreational fisheries that adopts a resilience management framework. Though we use inland recreational fisheries as an example, the general approach we take could apply to other socioecological systems.

WHY RESILIENCE IS IMPORTANT FOR MANAGEMENT OF INLAND RECREATIONAL FISHERIES

Recreational fisheries are considered socioecological systems because their outcomes depend at least on dynamic feedbacks between two primary components—fish and anglers. These dynamic feedbacks are created by angler-fish interactions that occur at multiple spatial (e.g., local, regional) and temporal (e.g., daily, annual) scales (Ward et al., 2016; Kaemingk et al., 2018; Matsumura et al., 2019; Murphy et al., 2019). Recreational-angler behavior, such as how much to fish, where to fish, and what fish to target, depends in part on fish populations, because catch-related attributes, like expected catch rate, size, and harvest, influence angler utility (Hunt, 2005; Hunt et al., 2019). These fishing behaviors, in turn, affect fish populations, mostly through fishing-related mortality and potentially sub-lethal effects (Welcomme et al., 2010). As a result, understanding of both fish ecology and human social behavior is needed to anticipate how environmental changes or management actions will affect common key recreational fisheries management objectives, like sustaining fishing effort that provides economic activity and supports local jobs, increasing satisfaction that anglers receive from fishing, and sustaining healthy abundances of fishes (Hunt et al., 2013).

Globally, management strategies and approaches of inland fisheries are understandably diverse, but there are commonalties (Cowx et al., 2010; Welcomme et al., 2010). Common recreational fisheries management actions include biological interventions, like invasive species removal (Zipkin et al., 2009; Coggins and Yard, 2010), as well as augmentative actions, like stocking hatchery-reared fish or restoring fish habitat (Taylor et al., 2017). Fisheries intervention most commonly includes restrictive measures to reduce fishing mortality, such as limiting harvest size, bag, season, and sometimes the fishing gear used. There is also an emphasis on communication methods to promote desired angler behavior (Li et al., 2010; Nguyen et al., 2012). Management actions are often imposed regionally, but in some cases, actions and regulations are applied to specific waters (of which some management regions may have thousands). This has prompted increasing calls for strategically designed spatial management plans (Lester et al., 2003; Hansen et al., 2015), though such plans remain rare (Carpenter and Brock, 2004; van Poorten and Camp, 2019). Given that recreational fisheries are coupled human and natural systems, decisions on which actions to take and at what spatial and temporal scales must consider both social and ecological components, as well as legal and political constraints and mandates. In practice, decisions often hinge on fish population abundance and dynamics, as well as stakeholder (typically angler) perceptions and preferences (Ward et al., 2016).

We believe that resilience concepts are particularly useful for sustaining key system services provided by inland recreational fisheries. Practically, inland recreational fisheries management ought to consider resilience to adopt better decision making (Grafton et al., 2019). Resilience is a characteristic of any system and thus intrinsically important for inland recreational fisheries, even if it is not always well-recognized. Any given fishery will have some inherent "degree" of resilience. This resilience will likely determine the overall influence managers may exert on the system, and the logistical challenges with, and viable strategies for, realizing that influence. Systems that appear to be characterized by greater resilience should require less management intervention, whereas systems with lesser resilience will require more management intervention to sustain (Walker et al., 2002). Failure to recognize the resilience of systems is likely to have costs. Management decisions about strategies adopted and actions taken have opportunity costs (time, funds, and social capital) that in some cases might be better allocated. Given the suite of anticipated perturbations to inland recreational fisheries, it is likely that most decision makers will be facing conflicting challenges from multiple objectives. Making management decisions in a resilience context could

better allocate scarce management resources, for example, by recognizing which types of management actions are best suited for attaining a desired state, or by recognizing when a desired state is practically unattainable.

CONCEPTUAL MODEL FOR OPERATIONALIZING RESILIENCE MANAGEMENT OF INLAND RECREATIONAL FISHERIES

Common resilience terms are defined (**Table 1**), but here we briefly explain the major aspects of resilience in the context of inland recreational fisheries. In recreational fisheries, resilience is a characteristic of a specific socioecological system (with soft spatial and temporal boundaries). For example, a system might be anglers targeting brown trout *Salmo trutta* and European grayling *Thymallus thymallus* Engerdal in Norway (Aas et al., 2000). Inherently, recreational fisheries systems will be affected by both social and ecological forces. Though in reality these forces are likely complex, here we consider them simply as the sum directional effects on the system, so for example, "positive social, negative ecological." The strength of these socioecological forces is expected to potentially interact in their influence on the system—but regardless will answer the question of "how would this system tend without management intervention?" Thus, the socioecological forces of the system should affect its overall resilience. Here, we consider the resilience of the system state can be described to exist in one of three stages of an adaptive cycle—structuring, structured, and restructuring, which together comprise the adaptive cycle through which a system can move. To managers, differences between a system in a stage of increasing resilience (building) and a system in a stage of decreasing resilience (collapsing) may be dramatic. The former could require substantially less intervention to sustain in the future, relative to the latter, which would require a reversal of ongoing processes.

The simplest conceptual model that we consider useful for characterizing a recreational fishery is illustrated (**Figures 1**, **2**) and outlined for practical application (**Box 1**). In short, the system is defined first by the management focus, then by the socioecological forces determining the system state, and finally by the resilience stage. In greater detail, the management focus will initially be defined by the governance filters, such as legislation or legal restraints, or political and government processes that are likely to constrain the focus to a reduced suite of fish and anglers. Examples of filters would be laws aimed at species protection (Endangered Species Act in the United States of America; Environment Protection and Biodiversity Conservation Act in Australia). Given these governance filters, the management focus is then narrowed to specific fish and anglers to be considered the target of management—the system. Finally, the management focus must be defined by preference. This preference defines if the management is focused on achieving a desired system or resisting an undesired system. For example, a system dominated by largemouth bass *Micropterus salmoides* might be desirable in the southeastern United States of America, but undesirable in Japan (Maezono and Miyashita, 2003) or subject to a mixed view in South Africa (see **Box 2**). While both fish and anglers are considered in the focus, the management preference may be focused more toward ecological (e.g., restoring native fish) or social (e.g., sustaining popular fisheries) ends, depending on the governance filters. We also note that management focus is used rather than management objective, recognizing that often the focus will incorporate more than one objective. Establishing these components of the management focus (filters, target fish and anglers, and management preference) can allow the system of interest to be defined.

The system can then be further characterized by the types of social and ecological forces acting on it, which we describe as the system state. Note that social and ecological forces may be synergistic and enforcing (both forces driving toward high resilience), antagonistic (one force driving high resilience, one low resilience), or synergistic and eroding (both driving low resilience). This creates four nodes (see **Figure 1**) for each of a desired (fore plane of **Figure 1**) and undesired (back plane of **Figure 1**) system. We describe a system on which management is focused and that has been characterized by socioecological forces as a "system state." A given system state may then be qualitatively described by the recognized resilience stages (structuring, structured, restructuring). These stages refer to the adaptive cycle, recognizing that stability breeds rigidity that will eventually tend toward reorganization. Finally, we describe specific system states and resilience stages in terms of the likely viable management strategies.

RESULTS

We believe that the utility of our conceptual approach lies in recognizing that certain combinations of management system preference, socioecological forces (state), and resilience stages will result in a limited number of viable management strategies. Thus, identifying these components of the resilience of these systems could support making decisions about management strategies and could forward management science through recognition of patterns in viable management strategies.

(i) Little intervention needed to achieve desired outcomes—A suite of state and stage combinations exist for which minimal management intervention is likely necessary to promote the preferred system. Desired system states with synergistic enforcing (+/+) social and ecological forces should sustain themselves with minimal intervention because the socioecological systems already tend toward the preferred management focus (**Table 2**, cells 1–2). Examples of such a structuring system state might have positive effects of recreational angling on conservation of management-preferred masheer *Tor* spp. in India (Pinder and Raghavan, 2013), or the emerging dominance of catch-and-release fishing for largemouth bass that occurred during the 1980s and 1990s in the United States of America, as angler behavior coupled with ecological traits resulted in desired states of high catch-rate largemouth bass fisheries (Myers et al., 2008). A reciprocal system state and resilience stage exists if an undesired system is restructuring under synergistic eroding forces [negative social and ecological, (–/–); **Table 3**, cell 12]. These forces ought

TABLE 1 | Terms and definitions.

Term	Definition
Adaptive cycle	Systems are not stationary, but rather oscillate between long periods of aggregation and transformation of resources and short periods of innovation.
Resilience	A measure of the amount of change needed to transform a system from one set of processes and structures to a different set (transformative features). A high-resilience state would require a substantial amount of energy to transform, whereas a low-resilience state would require a relatively small amount of energy to transform.
Panarchy	Interacting set of hierarchically structured scales that comprise socioecological systems. This framework connects adaptive cycles in a nested hierarchy.
Forces	Social and ecological processes that influence the specific system states and resilience stages. These processes may combine in additive or non-additive ways to enforce or erode resilience. For purposes of this paper and application to recreational fisheries, we characterize forces as synergistic (when forces align) and antagonistic (when forces oppose).
Management focus	The view through which sustainability of a system state and resilience stage is assessed and managed. Specifically, the management focus involves applying governance filters to select the specific system (fish and anglers of management interest) and then identify the desirability of the system state. The management focus will drive specific management objectives.
Management preference	The preferred state of the fishery system. This preference defines if the management is focused on achieving a desired system or resisting an undesired system.
Governance filters	Constraints external or not immediately inherent to the management focus and the coupled human-fish system. This might include legal stipulations (such as Endangered Species Act) or political economies and preferences—either of which may drive the management focus and eventually viable management strategies.
Target system	The group of anglers along with the species, suite of species, or size group of a species (e.g., walleye, native salmonids, or trophy largemouth bass) that are the subject of management objectives.
System state	Systems can exist under multiple sets of unique biotic and abiotic conditions. These alternative sets of conditions are non-transitory and therefore considered stable over relevant timescales. Due to social and ecological feedbacks, systems display resistance to shifts in sets of conditions and therefore tend to remain in one set of conditions until perturbations are large enough to cause a shift to another set of conditions.
Resilience stage	The characterization of a "general" system in terms of adaptive cycles (i.e., panarchy). Historically characterized by four stages; for purposes of this paper and application to recreational fisheries, we characterize with three stages (i.e., structuring, structured, and restructuring). Inherently, structuring and restructuring stages have lower resilience than structured stages.
Structuring	At a spatiotemporal scale relevant to management, the socioecological pattern or organization with respect to a focal species is developing. This is the growth or exploitation phase in the adaptive cycle.
Structured	At a spatiotemporal scale relevant to management, the socioecological pattern or organization with respect to a focal species established. This is the conservation phase in the adaptive cycle.
Restructuring	At a spatiotemporal scale relevant to management, the socioecological pattern or organization with respect to a focal species is collapsing and undergoing a reorganization. This is the release and reorganization phases in the adaptive cycle.

to act against the undesired state in a manner that hastens its restructuring, even absent management intervention. Cases where little action is needed for a specific management focus ought not to imply that management in general is unnecessary. Instead, it represents an opportunity for managers to shift resources toward other foci that may require more intervention and associated resources.

(ii) Little intervention needed because states and stages unlikely to occur and persist—A different suite of system states and resilience stages would likely require little intervention because they would be so rare and unlikely to persist. These consist of either desired or undesired states in synergistic eroding (–/–) stages and in structuring and structured stages (**Tables 2**, **3**, cells 10–11). Such cases are expected to be rare because it is not clear how the states could be structuring or structured given the coupled negative social and ecological forces. A special case may exist for cases where a desired or undesired state is in a restructuring stage despite synergistic building forces (+/+; **Tables 2**, **3**, cell 3). As with those described above, this situation seems unlikely to occur because the positive social and ecological forces seem unlikely to permit restructuring, unless there are strong forces beyond the recreational fishery socioecological system. For example, massive environmental or social changes from disasters, like war and disease epidemics, may physically restructure the environmental system and reprioritize the social system in ways that could relegate recreational fisheries management to irrelevance (e.g., World War II; Caddy, 2000).

(iii) Uncommon states and stages requiring action—Other system state and resilience stages are less common, but where they exist likely require intense management actions. These are cases where a desired state is restructuring under synergistic eroding (–/–) social and ecological forces (**Table 2**; 12), or where an undesired state under synergistic enforcing forces (+/+; **Table 3**, cells 1–2) is in a structuring or structured stage. The prominent examples of managing for a desired state despite eroding (–/–) social and ecological forces would exist when managing for a native species that is less popular and negatively affected by a more popular but invasive sportfish. For example, replacing the New Zealand non-native trout *Onchorhynchus* spp. and *Salmo* spp. fishery (currently managed by New Zealand Fish and Game) with the historical whitebait (*Galaxiidae*) fishery (currently managed by New Zealand Department of Conservation) would require a shift in social norms (i.e., convince anglers to prefer whitebait over trout) and

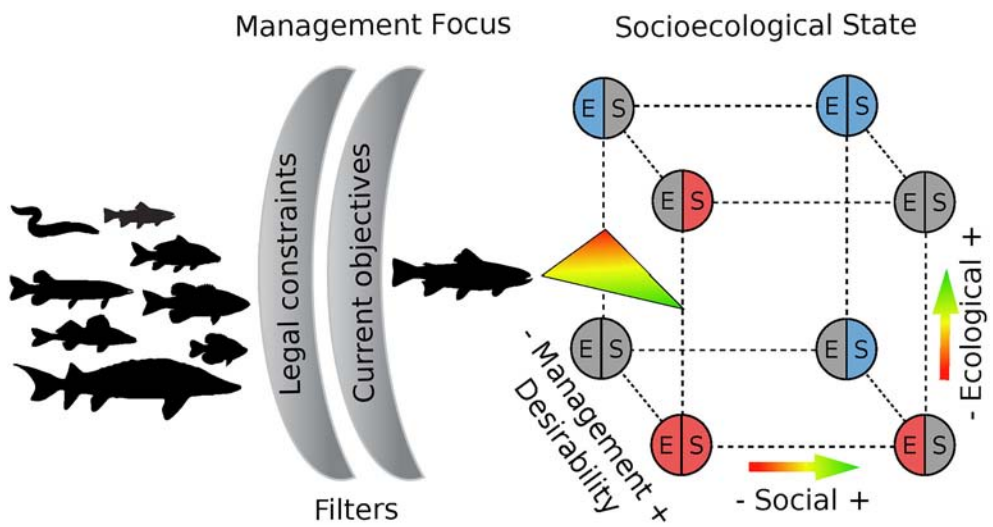


FIGURE 1 | Evaluating management resilience with respect to a focal species. Management resilience is evaluated with trout as the focal species filtered through legal constraint and current management objectives that help to determine the relevance of the species to management. The desirability of the species will fall along a spectrum (– to +) and can then be evaluated with respect to the spectrum of social (S) and ecological (E) forces (– to +). At the extremes, the nodes indicate the management action required to enhance resilience, with gray indicating no action, blue indicating management actions aimed at reducing the forcing component, and red indicating management actions aimed at enhancing the forcing component.

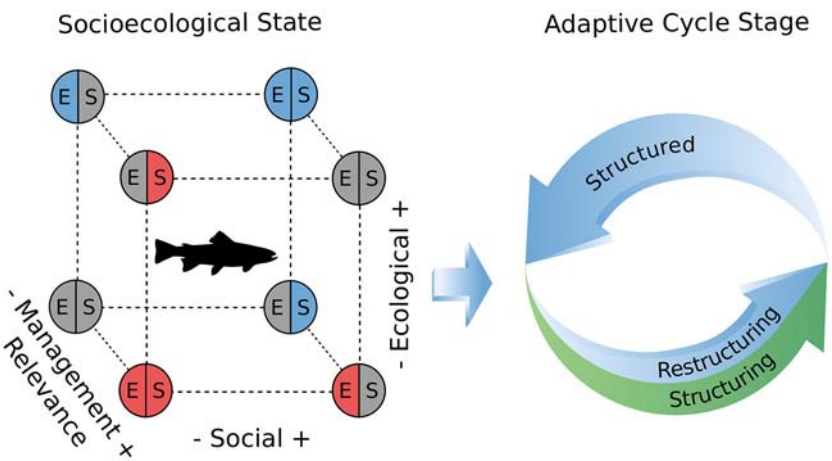


FIGURE 2 | Evaluating the system state with respect to a focal species once the node determining the nature of the action needed to maintain resilience in management is determined. The relevance of the species will fall along a spectrum (– to +) and can then be evaluated with respect to the spectrum of social (S) and ecological (E) forces (– to +). Systems are not stationary, and the malleability of the system state to management actions depends on the resilience stage (structuring, structured, restructuring) within the adaptive cycle. At the extremes, the nodes indicate the management action required to enhance resilience, with gray indicating no action, blue indicating management actions aimed at reducing the forcing component, and red indicating management actions aimed at enhancing the forcing component. The final options for management will depend on the system state.

involve intense biological intervention (i.e., trout eradication) to restore the native aquatic communities (Lintermans, 2000). One could argue that this is not possible (e.g., for the New Zealand Department of Conservation) and an unwise use of agency resources given the current socioecological resilience of the system. Such efforts, however, are not unprecedented, as intense trout removals occurred in the Colorado River to reduce mortality on the federally protected humpback chub *Gila cypha* (Coggins and Yard, 2010; **Box 3**). Where management agencies do elect to confront these challenges, there are two options: spatially explicit planning or changing the management focus (often by changing the management preference). Spatially explicit planning involves selecting certain waters in which to attempt to reverse the ecological forces, likely through intense intervention such as invasive species removals (Zipkin et al., 2009; Coggins and Yard, 2010).

BOX 1 | Steps for operationalizing.

We use the following steps to illustrate how the conceptual model could be used to operationalize management decisions. These steps can also be used to reveal missing and critical pieces of information that may require further research before proceeding. Some information was adopted from the Assessing Resilience in Socioecological Systems: Workbook for Practitioners (2010).

Step 1. ***Identify filters (legal constraints and current objectives)***

What are the legal constraints that should be considered?

What are the existing management objectives?

It is necessary to identify external and inherent legal constraints that may impede or promote certain management objectives and strategies. At the same time, it is imperative to identify the current management objectives that may be constrained or could direct the management focus.

Step 2. ***Identify management focus***.

What are the key socioecological forces of the system?

What are the spatial and temporal boundaries of the system?

What is the desirability of the system?

This step requires identification of key forces and associate interactions that are relevant to the management focus. These key components will have soft spatial and temporal boundaries that define the system. It is also important to recognize that the system will include cross-scale interactions that will be within and outside the established boundaries. Finally, the preferred state of the system should be clearly established given the management objectives.

Step 3. ***Define the current system state***.

What is the state of the system?

Is the state of the system desired or undesired?

A system can be described in terms of social and ecological forces that contribute to its current state. These social or ecological forces can create feedbacks that tend to support stability, unless social or ecological perturbations cause a shift into a new state. Therefore, it is important to characterize and understand how these social or ecological forces are influencing the current state. Defining the current system state then allows for discussion about whether it is desired or undesired, from both a social and ecological perspective.

Step 4. ***Evaluate the resilience stage of the system***.

Is the system in a structuring, structured, or restructuring stage?

It is important to recognize whether the system is in a structuring, structured, or restructuring stage in addition to defining the system state. Structured stages will inherently be more resilient than structuring and restructuring stages. Information concerning historical, current, and future states will be valuable for this step. Identifying the stage of the system is also essential for characterizing the system as being desired or undesired.

Step 5. ***Consider viable management options***.

What are viable management options given the current system state and resilience stage of the system?

A range of viable management options exist under different system states (**Tables 2**, **3**). Some system components may be enforcing resilience and others may be eroding resilience. Evaluating interactions of these forces allows for opportunity to effectively target social and ecological components and how they affect the system state. Careful consideration is necessary to explore these options and implement the most appropriate strategy, which in some cases may require very little action. However, hasty management actions could impede a favorable future system state without knowledge of the current system state and stage.

Alternatively, if management agencies consider the social and ecological forces insurmountable, agencies may elect to change their focus. Specifically, switching the management preference (from undesired to desired, and vice versa) converts these challenging scenarios to scenarios requiring little management action (described above). Changing the management focus will likely be difficult (especially depending on governance filters) but may prove more tenable in the long run. Embracing a new system state may allow for a greater breadth of viable management actions that accompany the "structuring stage" of an adaptive cycle. For example, many hydropower dam projects are planned for the Amazon, Congo, and Mekong river basins (Winemiller et al., 2016). Economic gain has been prioritized in these systems that will be accompanied with a loss in riverine species (Ziv et al., 2012; Anderson et al., 2018) and domination by lentic species. Cognizant of these looming changes, management agencies may elect to focus attention to these lentic species—such as promoting burgeoning fishing opportunities—rather than attempt to preserve the waning lotic fisheries.

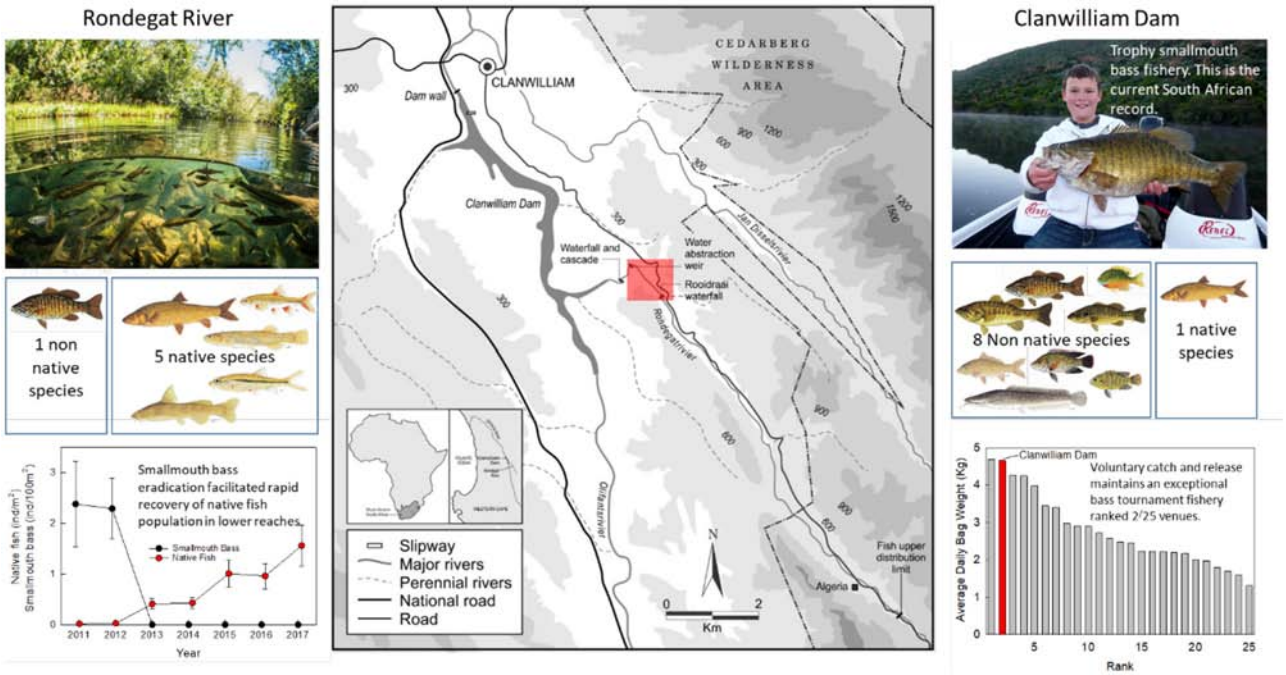
System states with opposing social and ecological forces (+/– or –/+) are likely to require the most intervention. For both desired and undesired states and across all stages (**Tables 2**, **3**, cells 4–9), there are essentially five management strategies that may be used singly or in combination.

(iv) Outreach and education—Endeavoring to alter stakeholder attitudes may be reasonable where social forces will oppose the management focus [i.e., –/+ on desired states (**Table 2**, cells 4–6), +/– on undesired states (**Table 3**, cells 7–9)]. Successfully changing what stakeholders want is likely to be challenging, but the potential benefit is altering the system forces so that the system state requires substantially less management intervention [e.g., shifting from –/+ to +/+ for a desired state (**Table 2**, cell 5 to cell 2)]. Outreach and education are sometimes the most feasible and may also be the least costly options, so in many cases, this will be the first management strategy to employ.

(v) Biological intervention—Biological interventions (e.g., stock enhancement, habitat restoration, invasive removal) are most appropriate with antagonistic forces where social forces align with management but are opposed by ecological forces

BOX 2 | Case study from Cape Fold Ecoregion, South Africa.

Many sport fishes, including several black bass (*Micropterus*) species have been stocked into South Africa's freshwater systems for the improvement of recreational angling opportunities (Ellender and Weyl, 2014). Smallmouth bass *Micropterus dolomieu* were introduced into South Africa in 1937 and rapidly established themselves in several freshwater systems (Khosa et al., 2019). Although this encouraged the development of recreational angling, which makes an important economic contribution to the South African Economy (Saayman et al., 2017), this species has resulted in the extirpation of endemic fishes (Van Der Walt et al., 2016). In the Cape Fold Ecoregion (CFE), a hotspot of regional fish diversity and endemism, predation by alien fishes is currently considered the primary threat to almost all of the endemic native fishes, and there is consensus among scientists and conservationists that this threat may jeopardize the long-term prospects for the endemic fauna (Ellender et al., 2017).



Similar to other parts of South Africa, conservation authorities in the CFE have been responsible for the management of freshwater fishes (Woodford et al., 2017). Thus, there has been a focus toward promoting conservation and very little emphasis on managing fisheries. In the case of smallmouth bass, management emphasizes the facilitation of fisheries in impoundments while trying to rehabilitate invaded headwater streams through directed eradication measures (Woodford et al., 2017). This is well-illustrated by their recent smallmouth bass eradication on the Rondegat River and their approach to the management of the Clanwilliam Dam in the Olifants River system (Weyl et al., 2014). From the perspective of the operationalization of resilience, the aim of the eradication project was to alter the structured, smallmouth bass-dominated state found in a reach of the Rondegat River. After the removal of smallmouth bass via the application of the piscicide rotenone, native fishes rapidly recolonized the rehabilitated section of river and within 2 years of the removal of smallmouth bass, the abundance and diversity was similar to that in the non-invaded reaches of the river (Weyl et al., 2014). In contrast to the conservation-based intervention in the Rondegat River, the management of the smallmouth bass-dominated fish fauna in Clanwilliam Dam has devolved to self-regulation by organized angler groups. Using the principle of voluntary release, the angler groups encouraged synergistic interaction of social and ecological forces and have maintained a stable state system for trophy smallmouth bass for decades. Indeed, Clanwilliam Dam ranked 2/25 with regard to catch weight and average fish size in an assessment of black bass tournaments held in southern Africa (Hargrove et al., 2015) and considered to be South Africa's premier smallmouth bass fishing destination with the national record of 3.52 kg captured in 2009. However, the recent illegal introduction of African sharptooth catfish *Clarias gariepinus* and an increase in the abundance of common carp *Cyprinus carpio* appear to have altered the ecological state of the fishery through bioturbation, and it appears that the stable "trophy smallmouth bass" state may be restructuring (Weyl pers. obs).

[i.e., +/− on desired systems (**Table 2**, cells 7–9), −/+ on undesired states (**Table 3**, cells 4–6)]. Examples might include removal of sea lamprey *Petromyzon marinus* in the Great Lakes of North America, where lamprey have been associated with negative effects on desired salmonid species (Coble et al., 1990). Managers must also consider that any biological intervention, but especially augmentative actions like stock enhancement, may well alter angler behavior and affect system outcomes (Camp et al., 2017).

A special case of biological intervention could occur if system states are deemed so precious and valuable that they demand (or legally require) all available resources to delay a likely inevitable collapse. These cases would likely be restricted to desired states with negative ecological forces in a restructuring stage (i.e., **Table 2** cell 9 and perhaps 12). Modern examples might include the exceptional measures taken to "rescue" (manually relocate) salmonids languishing in isolated pools of drying streams of western United States of America in the face of a climate

TABLE 2 | Examples and likely viable management strategies (in bold) for socioecological forces (rows) and resilience stages (columns) relevant for a desired management focus.

Forces	Structuring	Structured	Restructuring
+ Social/+ Ecological	1. +/+ on a building, desired system. Smallmouth bass and growing catch-and-release fishery in Pacific Northwest coastal rivers, USA. **Little action needed**.	2. +/+ on a stable, desired system. Catch-and-release oriented anglers and trophy largemouth bass in southern US ponds. **Little action needed**	3. +/+ on a collapsing, desired system. Rare, likely driven by forces beyond the recreational fishery socioecological system (SES) **Likely no viable mgmt. action**
– Social/+ Ecological	4. –/+ on a building, desired system. Coldwater/warmwater fisheries in Northern US lakes. **Outreach and education** **Fishery intervention** **Spatially explicit planning**	5. –/+ on a stable, desired system. Overfished recreational fisheries, such as Peacock bass in Brazil **Outreach and education** **Fishery intervention** **Spatially explicit planning**	6. –/+ on a collapsing, desired system. Potential recreational overfishing of Taimen in Mongolia. **Outreach and education** **Fishery intervention** **Spatially explicit planning**
+ Social/– Ecological	7. +/– on a building, desired system Naturalizing populations of introduced trout in Europe **Biological intervention** **Spatially explicit planning**	8. +/– on a stable, desired system Put-and-take stocked salmonid fisheries **Biological intervention** **Spatially explicit planning**	9. +/– on a collapsing desired system Rescuing native salmonids in western US streams affected by drought and climate change. **Extreme biological intervention** **Spatially explicit planning**
– Social/– Ecological	10. –/– on a building desired system Rare and unlikely to persist **N/A**	11. –/– on a stable desired system Rare and unlikely to persist **N/A**	12. –/– on a collapsing desired system Native cyprinids facing climate change and more popular, non-native trout in the Grand Canyon, USA. **Extreme biological intervention** **Spatially explicit planning** **Change mgmt. objectives**

1. In some rivers of Pacific Northwest, introduced non-native smallmouth bass Micropterus dolomieu have developed as a socioeconomically important recreational fishery that is desired by many anglers and to some extent by management agencies, though there may be negative effects on native salmonid populations (Carey et al., 2011). The popularity of smallmouth bass with anglers, coupled with their apparent ecological advantage in these systems, suggests that little management action is needed (as long as this new system is desired).
2. Catch-and-release ethic among trophy bass anglers produces a bass size structure that is likely associated with a high-quality fishing experience desired by anglers and management agencies alike in southern US lakes and ponds (Myers et al., 2008). Often little fisheries management intervention is needed.
3. No clear examples are apparent from primary literature, but a number of studies describe in passing the suspending of fisheries management actions associated with international conflict, such as World War II (Caddy, 2000).
4. Waters that were traditionally managed more for coldwater species (Esox spp., walleye Sander vitreus; Olson and Cunningham, 1989) are increasingly producing excellent warmwater fishing for species such as largemouth bass Micropterus salmoides (Sharma et al., 2007). Though management agencies may now prefer to manage for warmwater species, this is resisted by other anglers who prefer coldwater species. Here management might consider outreach and education to convert anglers to warmwater fisheries, regulations that encourage warmwater fishing, or managing only certain waters for warmwater.
5. Overfished inland recreational fisheries, such as the peacock bass (Cichla spp.) in Amazonia waters where they have been heavily exploited by (often tourist) anglers (Allan et al., 2005; Campos and Freitas, 2014). More restrictive harvest or even effort management may be needed if education (e.g., importance of returning large fish) fails to stem overharvest.
6. Growing fishing effort from tourist anglers targeting taimen Hucho tiamen in Mongolia, where the desired system is a sustained taimen population (Jensen et al., 2009; Golden et al., 2019). Though ecological conditions may still promote healthy taimen populations, it is likely that fisheries management would need to constrain harvest or even fishing effort if there is non-negligible catch and release mortality (Jensen et al., 2009).
7. Introduced but naturalizing populations of fish, such as rainbow trout throughout much of Europe constitute a system where social forces (popularity of rainbow trout) can lead to structuring states (trout fisheries) in systems that may not be ecologically well-suited (Stanković et al., 2015).
8. Put-and-take salmonid fisheries (in which catchable-sized fish are stocked repeatedly in waters in which they cannot spawn and sometimes cannot survive stresses of summer or winter) are popular worldwide and can produce stable fishery systems where their popularity convinces managers to sustain stocking programs, as typically ecological conditions would not permit self-sustaining populations (Patterson and Sullivan, 2013). Here the stocking represents the biological intervention, which also likely occurs in a spatially explicit manner (i.e., only "suitable" lakes are stocked).
9. Manual relocation ("rescuing") native salmonid populations in drought-ridden streams of western USA (Beebe, 2019). Intensive biological intervention may slow the restructuring of the desired state (native salmonid fish and fisheries).
10–11. Rare and unlikely to persist; no clear examples.
*12. In the Colorado River that flows through the Grand Canyon of the western United States of America, native cyprinid fisheries may be declining as additional water and hydroelectric requirements increase coupled with popular but non-native salmonid. Management options have tended toward extreme intervention (salmonid removals, flow alterations; see **Box 3**) (Runge et al., 2018).*

that is unsuitable for a species (Beebe, 2019), or efforts to sustain humback chub (**Box 3**). Such attempts may have a great resource cost, but could produce social and political support for a particular imperiled system that provides ecological benefits for other less threatened taxa (Moyle et al., 1992; Moyle and Moyle, 1995), or benefit future management and conservation efforts. For example, public support for declining (and now extinct) passenger pigeon *Ectopistes migratorius* populations paved the way for the United States Endangered Species Act. Discontinued management support for a socially highly valued system that is destined for collapse could result in a loss of public support and trust.

(vi) Fishery intervention—Management actions intended to alter the fishery may be warranted in states with antagonistic forces where ecological forces align with management objectives but are opposed by social forces [i.e., –/+ on desired systems (**Table 2**, cells 4–6), +/– on undesired states (**Table 3**, cells 7–9)]. Classic fishery intervention would be meant to prevent, or reverse overfishing, such as described by Post et al. (2008) in western Canada trout fisheries, or may be mounting for newer

TABLE 3 | Examples and likely viable management strategies for socioecological forces (rows) and resilience stages (columns) relevant for an undesired management focus.

Forces	Structuring	Structured	Restructuring
+ Social/+ Ecological	1. +/+ on a building undesired system. Smallmouth bass and growing catch-and-release fishery in Pacific Northwest coastal rivers, USA. **Spatially explicit planning** **Change mgmt. objectives**	2. +/+ on a stable undesired system. Catch-and-release oriented trout anglers and the whitebait fishery in New Zealand where undesired state is introduced salmonids. **Spatially explicit planning** **Change mgmt. objectives**	3. +/+ on a collapsing undesired system. Rare, likely driven by forces beyond the recreational fishery **Likely no viable mgmt. action**
– Social/+ Ecological	4. –/+ on a building undesired system. Unwanted establishing invasive Asian carp and anglers in the Mississippi River, USA **Biological intervention** **Spatially explicit planning**	5. –/+ on a stable undesired system. Public and sea lamprey in Great Lakes, USA. **Biological intervention** **Spatially explicit planning**	6. –/+ on a collapsing undesired system. Overfishing introduced Nile Perch in Lake Victoria in East Africa. Examples relatively rare. **Outreach and education** **Spatially explicit planning**
+ Social/– Ecological	7. +/– on a building undesired system. Angler introductions of non-native species in Spain; overfishing. **Outreach and education** **Fishery intervention**	8. +/– on a stable, undesired system. Non-native largemouth bass and anglers in Japan. **Outreach and education** **Fishery intervention**	9. +/– on a collapsing undesired system. Whirling disease disproportionately affecting non-native salmonids in northeastern United States of America. **Outreach and education** **Fishery intervention**
– Social/– Ecological	10. –/– on a building undesired system. Rare and unlikely to persist **N/A**	11. –/– on a stable, undesired system. Rare and unlikely to persist **N/A**	12. –/– on a collapsing undesired system. Rare **Little action needed**

1. System: Introduced and popular smallmouth bass fisheries (undesired system) in coastal rivers of Pacific Northwest, USA. Situation: In some rivers of Pacific Northwest, introduced non-native smallmouth bass have developed as a socioeconomically important recreational fishery that is desired by many anglers but may be undesired by management agencies seeking to preserve native salmonids (Fritts and Pearsons, 2004). The popularity of smallmouth bass with anglers, coupled with their apparent ecological advantage in these systems suggests either management intervention in select systems, or wholescale alteration of management objectives (i.e., to "desire" the building smallmouth bass state).

2. Non-native salmonids introduced to New Zealand waters are undesired (by some management agencies) because of their deleterious effect on the native whitebait (galaxiidae) populations (Lintermans, 2000). Non-native trout are popular sportfish for local and tourist recreational fishery that is largely catch-and-release. Managing for native fish in certain waters may be tenable.

3. No clear examples are apparent from primary literature, but a number of studies describe in passing the suspending of fisheries management actions associated with international conflict, such as World War II (Caddy, 2000).

4. Invasive Asian carp, which are not readily caught on terminal tackle, have rapidly expanding populations throughout the river basin and are outcompeting native species sought by recreational anglers. Relevant management actions include removal of invasive species or motivating fishery exploitation (Tsehaye et al., 2013).

5. Sea lamprey are considered a pest organism in the Great Lakes of North America, where lamprey have been associated with negative effects on desired salmonid species (Coble et al., 1990). Primary management actions include removal with the intent to eradicate or limit population.

6. Overfishing of introduced Nile perch Lates niloticus may correlate with increased smaller native fish traditionally targeted in Lake Victoria, East Africa. This example depends on agencies classifying Nile Perch as an undesired system, which is not likely unanimous (as many may prefer the introduced species for its economic effects (Mkumbo and Marshall, 2015). While spatial planning may be applicable in many systems, it may not be useful in this large lake that borders three countries.

7. Angler-introduced species in freshwaters of Spain may be leading to negative effects on wild fish (Elvira and Almodóvar, 2001). Another common, general example would be mounting overfishing, as apparently occurred in Northwest Canada's lake fisheries for salmonids (Post et al., 2008).

8. Management efforts are underway to eradicate largemouth bass in Japan because this invasive species has caused and is causing harm to native fishes (Nishizawa et al., 2006). Even so, the popularity of bass fishing in Japan continues to increase, especially among catch-and-release anglers from around the world.

9. Whirling disease disproportionately affected non-native rainbow trout and brown trout compared to salmonids native to northeastern United States of America, brook trout Salvelinus fontinalis and lake trout Salvelinus namaycush, and for a short time, it appeared that this disease might shift systems away from non-native trout (though these non-natives would have still been the desired system by many if not most management agencies; Hulbert, 1996). An alternative example would be cases where a nutrient enriched lake (undesired state) can be restored ecologically, but doing so would lower fishery productivity (i.e., anglers and social forces would prefer the enriched, undesired system state). This roughly was exemplified by the Kootenay Lake fertilization experiment in western Canada (Ashley et al., 1997).

10–12. Rare; no clear examples.

destination fisheries like peacock bass *Cichla* spp. and arapaima *Arapaima* spp. of Amazonia, goliath tigerfish *Hydrocynus* spp. of the Congo river basin, or tiamen *Hucho taimen* of Mongolia (Allan et al., 2005; Post et al., 2008; Jensen et al., 2009; Campos and Freitas, 2014; Lennox et al., 2018). Less common, but feasible fishery interventions would include encouraging overharvest of species associated with an undesired state (e.g., Asian carp *Hypophthalmichthys* spp. in the Mississippi River system; Galperin and Kuebbing, 2013; Varble and Secchi, 2013). This would likely involve melding classic fishery management actions (e.g., relaxation or elimination of harvest and gear restrictions) with outreach and education approaches to encourage different angler behavior, or perhaps supporting markets for commercial exploitation of the undesired species (Catalano and Allen, 2011; Nuñez et al., 2012). It should be noted that this induced-overfishing type of intervention might occur in system states and resilience stages typically characterized by biological intervention (e.g., **Table 3**, cell 4). Thus, the delineations of biological vs.

BOX 3 | A case study: The Grand Canyon, United States of America.

Managing for resilience when everything is complicated: the case of the Grand Canyon

A principle from resilience applications to natural resource management is the importance of probing models until they fail (Holling, 1973; Holling and Meffe, 1996). This can reveal tenuous assumptions that may lead to costly mistakes. It is prudent to confront the conceptual model we present here with an especially challenging and complicated scenario. One such example is the management of the fish and fisheries in the lower Colorado River as it flows through a series of iconic canyons (Glen, Marble, and Grand canyons) and wilderness reaches between Glen Canyon Dam and the western edge of Grand Canyon National Park upstream of Lake Mead in the western United States of America. These complexities include the following:

- Major alternations to river discharge due to large hydroelectric dams that provide power and water to millions of citizens
- Complex governance at interstate and international levels including seven recognized American Indian tribes.
- Multiple competing and likely alternative fish communities: native cyprinids including the endangered humpback chub *Gila cypha* and introduced non-native salmonids that support economically valuable recreational fisheries but may cause deleterious impacts to native fish communities (Korman et al., 2015). Expanding risk of range expansion from warmwater non-native species that may also have negative impacts to native species.
- Complex and competing interests of stakeholders including wilderness hiking and rafting, native fish, unique river ecosystem, hydropower production, and water storage and delivery.
- These interests all occur within an area that is the ancestral home to multiple American Indian Tribes who value the economic, cultural, and spiritual components of the region.

Classifying the system using our conceptual model

This system would clearly have multiple filters shaping the management foci—federal Endangered Species Act laws requiring action to prevent extinction of native fish, human well-being associated with continued production of electricity and in other parts of the system, drinking water, and American Indian rights (Melis et al., 2015). Beyond these, our conceptual framework would first consider the Grand Canyon system as separate desired and undesired system states. One desired system state would be the native cyprinid community. This would likely have some positive (humans preferring a "natural" systems) but also some negative social forces (humans preferring to catch non-native salmonids). Ecological forces currently would be negative because the altered flow and thermal regimes may allow non-native salmonids and other fish to out-compete native cyprinids (Coggins and Yard, 2010). So this would place the native cyprinid system state in either a synergistic eroding or restructuring stage (**Table 2**, cell 12), or, if one believes the social forces tip toward preserving native fish, in an antagonistic (+/–) restructuring stage (**Table 2**, cell 9). A separate desired state would be the non-native salmonids. This would largely represent the inverse of the native state—with positive ecological forces and either negative or positive social forces in likely a structured stage (so **Table 2**, cells 2 or 5).

Examining if the management advice makes sense

If the native cyprinid system is preferred, our conceptual model suggests that it should be pursued by biological intervention, spatially explicit planning, or a change in management objectives (**Table 2**, cells 9 and 12). Biological intervention does in fact occur, with non-native removals and flow alterations designed to improve habitat, but may forfeit some hydropower production (Runge et al., 2018). In addition to being logistically challenging, non-native removals have also been criticized by American Indian tribes, whereas flow alterations also impose costs and are unlikely to dislodge non-native species (Runge et al., 2018).

If the non-native system is preferred, the most likely state and stage would correspond to little management action (**Table 2**, cell 2) or at most attempts to change stakeholder perceptions or to adopt spatially explicit management (**Table 2**, cell 5). This does appear to largely match what has been considered (Runge et al., 2018).

Though the conceptual model appears reasonable for applying to even this complex system, two weaknesses are highlighted. First, the conceptual model does not explicitly force the user to consider how actions advised in the management pursuit on one desired state will affect those of another. This is implied by the recommendations for spatially explicit management (e.g., **Table 2**, cells 5 and 9), where the antagonistic nature of social and ecological forces would suggest doing different things in different places is ideal. Second, the conceptual approach does not provide specific advice for how to implement the broad management strategies suggested. This may be unfixable, as such detailed advice is unlikely useful across many systems. In the case of the Grand Canyon, the external filters (multiple sovereign states, legal mandates) describe a system too complex for agency-specific management and one in which no management decisions can reasonably reconcile the multiple objectives and values (Schmidt et al., 1998).

fishery intervention need not be rigid, and often biological and fishery interventions will be combined as a management strategy (e.g., removal of undesired non-native species could be combined with deregulating their harvest or restricting their voluntary catch and release).

(vii) Spatially explicit planning—The above management strategies may alone be insufficient to sustain desired and stave off undesired states. It may be necessary to consider spatially explicit planning—an application of marine spatial planning approaches of managing for different purposes in different places. This could be for two separate reasons. If social forces will oppose the management focus, it may make sense to designate certain discrete waters for whatever system stakeholders desire, even if it is counter to the management focus; for example, stocking non-native rainbow trout *Oncorhynchus mykiss* in some discrete waters while leaving other waters for native species. Alternatively, if social forces align with management foci, spatially explicit management may be needed if resources limit the biological intervention to a subset of waters. For example, resources for invasive species removal or native stocking may require focusing these actions on only some waters.

In summary, there seem to exist two groups of system state and resilience stages—those that do not require management action, either because (i) they already align with management objectives or (ii) are unlikely to occur and persist, and then those requiring management actions. Of the latter, there seem to exist relatively few options for shifting the system against the net effect of social and ecological forces. In short, managers may (iii) adopt a different management preference or focus, (iv) endeavor to change social norms, (v) engage in ongoing biological intervention (e.g., invasive species removal), (vi) engage in fishery intervention, or (vii) adopt landscape-level management approaches focusing on achieving different systems or states in different waters.

DISCUSSION

Operationalizing resilience provides management agencies a framework to (1) evaluate the state of a system (Beisner et al., 2003), (2) predict stage cycles a system state may undergo (Gunderson and Holling, 2002), (3) pinpoint which forces could shift a system to a different state (Walker et al., 2004), and (4) determine the management action (i.e., amount of disturbance) required to achieve a desired state (Suding et al., 2004). Management decisions, particularly in the developing world, are made with limited resources, and thus, opportunity costs must be considered. Incorporating resilience into management practices will enable diverse stakeholders the ability to make informed decisions that recognize costs, challenges, and process interactions associated with management goals and objectives.

This framework is designed to initially focus on singular management foci, but in many cases, management agencies will find themselves facing multiple objectives. How this should be handled will depend largely on how these multiple management foci interact. Some system states and resilience stages may complement each other. For example, if a given management focus requires little management intervention, recognizing this should make resources more available for management objectives. A realistic example might be in the southeastern United States of America, where the primary inland recreational fisheries management focus for most regions is ensuring a desired largemouth bass fishery is sustained. However, the ecology of largemouth bass combined with extreme voluntary catch and release angler behavior likely results in +/+ social and ecological forces on a desired state and structured stage. Management agencies in such situations may redirect some resources toward additional management foci, such as less prominent but still important fisheries, rare but untargeted fisheries, or groups of anglers who may be underserved (e.g., shore-based or minority anglers). Where multiple management foci do not complement in this manner, resources must be divided. The common tools for addressing these cases exist in decision science, from initial multi-attribute decision-making processes, to more modern Structured Decision Making procedures (Kleindorfer et al., 1993).

A particular but common case of managing for multiple system states simultaneously is where the desired states actively conflict with each other or compete. Competing objectives is no new challenge and is common in inland recreational fisheries (e.g., managing for native non-sport fish and non-native sportfish, or managing for high catch rates and trophy fish). Where there exist multiple discrete or near-discrete waters, the most likely way to address this is spatially explicit management that divides systems out and manages them with separate objectives. For example, managing for angler satisfaction through fish stocking whilst mitigating negative effects on wild fish stocks may be difficult to achieve within the same system (Pister, 2001). In this case, a subset of systems could be managed for anglers (i.e., stocked) and the remaining systems managed for wild stocks or genetic variation (i.e., not stocked). In the developing world, a subset of systems could be managed to serve food security needs (for recreational anglers and subsistence fishers) and others for recreational fishing tourism.

Of course, there are examples where a single or rather indivisible water hosts multiple competing management foci that are unlikely to be simultaneously achieved. For example, collectively managing for salmonids *Oncorhynchus* spp. and smallmouth bass *M. dolomieu* in Pacific Northwest rivers will likely be futile. A decision must be made to manage for either smallmouth bass, salmonids, or some other structured state. Pacific Northwest fisheries appear to be in a restructuring stage given a focal lens of salmonids, whereas they appear to be in a structuring stage given a focal lens of smallmouth bass. Anthropogenic alterations of habitat (e.g., dams) and climate change have led to an increase in smallmouth bass abundance; smallmouth bass consume salmonids and compete for available resources (Carey et al., 2011). A change in salmonid or smallmouth bass populations will likely lead to a different system state and resilience stage (i.e., top system predator), but the amount of management costs or disturbance required to shift the system from a "smallmouth bass" to a "salmonid" state will be drastically different from the management costs to shift the system from a "salmonid" to a "smallmouth bass" state. In a developing world example, collectively managing a gillnet-based food fishery and an exclusive tourist, trophy fishery for large *Labeobarbus* species in a large South African impoundment (Vanderkloof) will also likely be futile. This is not only because the emerging harvest fishery may drive the system into a restructuring stage, but also from a social perspective as extensive gillnetting and exclusive tourist angling destinations for trophy fishes are not compatible. Though there is increasing political pressure to expand the gillnet-based food fishery, the characteristically slow growth of the large *Labeobarbus* (Ellender et al., 2012; Gerber et al., 2012) will most likely not support a harvest fishery state and this restructuring will not lead to a highly resilient fishery. Ultimately, the choice of state and resilience stage in the developing world will need to consider how local communities will benefit most from a particular resource, and in this case, it is anticipated that managers will desire to restructure the fishery toward a trophy *Labeobarbus* state and encourage community development through active investment in the tourism industry. Regardless of whether a manager operates in the developed or developing world, placing decisions in a resilience management framework will afford practical guidance for difficult and complex socioecological problems such as these.

There exist a number of limitations of how this work can be used to better integrate resilience concepts in management. Despite our efforts, this work likely misses important developments of inland recreational fisheries taking place in certain parts of the world, especially Asia. Also, some of the broad management strategies described will be exceptionally difficult to accomplish. For example, changing stakeholder attitudes and behaviors through outreach and education will be exceptionally difficult. Though the tools to systematically affect human perceptions, attitudes, and actions are almost certainly more powerful now than they have ever been before (i.e., social networks, big data, and machine-learning approaches), the ethical and social capital implications of attempting to do so have not been well-explored. Similarly, changing management

objectives is not easy and will require flexible governance systems and ample social, political, and economic capital. This is likely to engender pushback from managers. Another challenge is the uncertainty associated with assessing system states and resilience stages. The uncertainty associated with restructuring and potentially structuring stages introduces an additional level of uncertainty into management. If the stage of the system is unclear, the dynamic system must be evaluated and management goals established. If the emerging system is sufficiently novel, multiple tactics—social or ecological—may exist. In such instances, provided a sufficient time frame, managers may wish to employ adaptive strategies to select the desired management approach. This iterative process may result in an evolution of management objectives as the new system emerges.

Two deeper limitations require particular attention. First, the conceptual model implies managers can understand how social and ecological forces act on the system, which is necessary to define the system state. Sometimes this will be obvious, but other times, it may not be—especially when multiple stakeholder groups want and act in opposite ways (e.g., anglers preferring wild catch-and-release fisheries and those wanting put-and-take fisheries, or traditional recreational fisheries to supplement food and burgeoning destination-fishing intended to attract tourists). This leads to the second, deeper flaw with our conceptual model—it does not provide insight as to how to select one system focus over another (i.e., defining the management focus). This could be trivial in simple systems with homogeneous anglers and minimal conflict with non-anglers. But in other systems where multiple angler and non-angler stakeholders want fish or their habitat (e.g., water) for competing uses, it will be complex (Schmidt et al., 1998; Floyd et al., 2006; **Box 3**). And everywhere, the definition of focus will be affected by the power different stakeholder and governance entities hold (Daedlow et al., 2011, 2013; May, 2016). Unfortunately, we know of no agreed-upon metric whereby managers (of any natural resource) can determine which user group's desire should be prioritized. In many countries, this is evaluated by courts and litigation. Unable to resolve this limitation, we can only emphasize its importance.

Emerging from this work is the recognition of the role of spatial and temporal scale when considering resilience management of recreational fisheries; management of individual discrete waters may not require the same approach as management at a regional or landscape scale—at least, the latter would allow for some different approaches. A paradigm shift from water-specific management in isolation to water-specific management within the landscape context of other, surrounding waters (within and outside political boundaries of interest) is in order. In essence, design for adaptability with the explicit recognition that it is not possible to meet all socioecological needs within a single system. Having said this, we also recognize that at some time scale, all systems are in a panarchical cycle. There are many institutional procedures (e.g., license sales, political desires to provide similar opportunities among spatially distributed constituents) in place to reinforce regional management. Even so, we acknowledge that the potential costs (decision making, monitoring, and enforcement) of implementing a more detailed spatial management may be great. However, the cost of exploring such options is minimal and may greatly enhance the understanding of the socioecological system being managed. The challenge is to develop creative ways to think about management actions (habitat manipulations, stocking, regulations) and how they impact the resilience of a system by (1) breaking down resilience of social or ecological forces of an undesired state to allow the system to reorganize into a different and hopefully desired state and (2) reinforcing the resilience of social or ecological forces of a desired state to sustain the system in that state.

Systems could reside in multiple different system states and resilience stages within a management unit (e.g., regional fishery; Martin and Pope, 2011; Chizinski et al., 2014; Martin et al., 2017), which affords the opportunity to focus efforts on a subset of systems, perhaps based on ecosystem size (Kaemingk et al., 2019). Again, a resilience management framework would facilitate prioritizing which systems should be selected based on their system state and resilience stage as well as available resources. This becomes fairly straightforward if most systems are structured in desirable states (i.e., minimal inputs needed), and only a few are in a structuring or restructuring stages that will lead to undesirable states. Some United States management units have a small subset of waters infected by invasive mussels that can cause economical damage and ecological harm (Kraft and Johnson, 2000). Management efforts, albeit costly, could be prioritized to remove or prevent the spread of these mussels to other systems within a management unit.

SYNTHESIS AND LOOKING FORWARD

Viewing resilience as a characteristic of inland recreational fisheries is attractive for management and conservation efforts. Further categorizing these resilience characteristics provided a framework for operationalizing resilience management for conservation of inland recreational fisheries (**Figures 1, 2**, **Tables 2**, **3**) by recognizing the management strategies likely viable for given system states and resilience stages. Few options exist for shifting a fishery system against socioecological forces. In short, managers may (1) adopt a different ecological system as the management objective, (2) endeavor to change social norms, (3) engage in ongoing biological intervention (e.g., invasive species removal), (4) engage in fishery intervention, or (5) adopt landscape-level management approaches focusing on achieving different systems in different waters. The latter options are suitable under the greatest number of system-state and resilience-stage combinations and are uniquely relevant to inland recreational fisheries given the existence of discrete waters and the general inability of most fishes to traverse terrestrial environments.

We envision a future world in which management agencies developed resilience plans for desired and undesired states of their systems. The plans would identify and rank potential system states (including socioecological forces) and include potential actions to be implemented for each combination of resilience stage and system state. These plans would result in more efficient objectives and would actually prioritize actions that focus on sustaining desired system states rather than optimizing services of those states at any given time.

AUTHOR CONTRIBUTIONS

KP was invited to submit a contribution to this special feature and assembled the team of authors. EC, KP, MK, RA, and WMP devised the conceptual model presented herein. EC, MK, RA, WMP, WEP, OW, and KP contributed to the writing of the manuscript.

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Integrating Ecosystem Resilience and Resistance Into Decision Support Tools for Multi-Scale Population Management of a Sagebrush Indicator Species

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Imperiled sagebrush (*Artemisia* spp.) ecosystems of western North America are experiencing unprecedented conservation planning efforts. Advances in decision-support tools operationalize concepts of ecosystem resilience by quantitatively linking spatially explicit variation in soil and plant processes to outcomes of biotic and abiotic disturbances. However, failure to consider higher trophic-level fauna of conservation concern in these tools can hinder efforts to operationalize resilience owing to spatiotemporal lags between slower reorganization of plant and soil processes following disturbance, and faster behavioral and demographic responses of fauna to disturbance. Here, we provide multi-scale examples of decision-support tools for management and restoration actions that evaluate general resilience mapped to variation in soil moisture and temperature regimes through new lenses of habitat selection and population performance responses for an at-risk obligate species to sagebrush ecosystems, the greater sage-grouse (*Centrocercus urophasianus*). We then briefly describe general pathways going forward for more explicit integration of sage-grouse fitness with factors influencing variation in sagebrush resilience to disturbance and resistance to invasive species (e.g., annual grasses). The intended product of these efforts is a more targeted operational definition of resilience for managers by using quantifiable metrics that help limit chances of spatiotemporal mismatches among restoration responses owing to differences in engineering resilience between sagebrush ecosystem processes and sage-grouse population dynamics. Moreover, spatial resilience can be promoted though explicit consideration of sage-grouse and sagebrush predicted responses to active and passive management treatments across space and time. We describe tools that include multi-scale geospatial overlays and simulation analyses of post-disturbance land cover recovery aimed at prioritizing primary threats to sagebrush ecosystems in the Great Basin in the western portion of sage-grouse range (i.e., grass-fire cycles and conifer expansion), but underlying concepts have broader application to a range of ecosystems.

Keywords: ***Artemesia* conservation planning, *Centrocercus urophasianus*, conifer expansion, sage-grouse, suitability, wildfire, umbrella species**

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INTRODUCTION

Practitioners of restoration ecology continue to build upon the foundational concepts of ecological resilience (Holling, 1973), whereby pathways among ecosystem processes reorganize their structure following disturbances of various strength to either remain within an original state, shift among transient states, or fall into an alternative and possibly hysteretic state if thresholds for disruption are surpassed and return pathways are altered (Scheffer et al., 2001; Beisner et al., 2003; Suding et al., 2004; Standish et al., 2014). Arguably the largest impetus for this work is an increasing recognition of widespread changes to disturbance regimes, climate, and species pools occurring at local to global scales (Seastedt et al., 2008). These changes associate with a subsequent rise of novel ecosystems that are highly resilient against restoration efforts, owing to a deep and narrow basin of attraction in the alternative state, and are very difficult to manage (Hobbs et al., 2009). There is also now a greater appreciation of context dependency that seeks to recognize and identify the biotic and abiotic conditions that largely dictate the chances of restoration success (Eviner and Hawkes, 2008), and calls for more rigorous monitoring efforts of restoration outcomes with appropriate metrics over meaningful time periods (Suding, 2011).

Accordingly, managers, policy makers, and resource-user groups tasked with ecosystem stewardship during this challenging era of restoration (Suding, 2011) require tractable tools that bring resilience out of the conceptual realm and into effective implementation. The paradigm of "operationalizing resilience" has been proposed as means of achieving this daunting task and can be a powerful tool in the fight against permanent degradation and loss of vulnerable ecosystems world-wide (Suding, 2011; Angeler and Allen, 2016; Chambers et al., 2019a). Broad-scale efforts to make resilience concepts operational have occurred largely through socio-ecological frameworks such as the Millennium Ecosystem Assessment (Carpenter et al., 2009), the Resilience Alliance (2010), and Arctic stewardship (Chapin et al., 2015). However, their effectiveness is limited somewhat by a reliance on stakeholder-led iterative and qualitative processes rather than quantitative tools that predictively model outcomes of specific passive or active actions (Angeler and Allen, 2016). Thus, operationalizing resilience in restoration remains relatively nascent due to persistent challenges with quantification of factors influencing resilience under complex settings (Suding, 2011; Perring et al., 2015); and hence, the papers in this special issue. Another set of challenges toward operationalization are the multiple distinct, yet interconnected types of resilience that require clear definition to minimize confusion. **Table 1** provides a brief description of the types of resilience invoked herein following definitions of Angeler and Allen (2016) and Chambers et al. (2019a).

TABLE 1 | Brief definitions of types of resilience described for examples used in this paper following Angeler and Allen (2016) and Chambers et al. (2019a).

Resilience type	Definition
General	Generic description of properties that allow maintenance of fundamental function and structure following disturbance, useful across broad scales
Ecological	Amount of energy (e.g., stress, disturbance) needed to drive a system to a new state, or capacity of a system to absorb that energy and regain fundamental structure or remain unchanged
Engineering	Time to recovery to previous or desired state (e.g., recovery rate)
Spatial	How attributes affecting resilience vary across space and time; considers landscape composition and configuration

Operationalizing Resilience in Sagebrush Ecosystems

The iconic sagebrush (*Artemisia* spp.) biome of western North America spans 11 states and 2 provinces along varied hydrographic, floristic, and elevation gradients, harbors a diverse species assemblage of flora and fauna, and provides economic livelihoods for a diverse range of user groups including ranchers and outdoor enthusiasts (Suring et al., 2005; Davies et al., 2011). It is also a biome at risk, having contracted by over 50% post-European settlement (Schroeder et al., 2004) owing to multitude of factors including energy development, cropland conversion, improper livestock grazing, wildfire, and invasive species (U.S. Fish and Wildlife Service, 2015a). Concomitantly, over 350 plant and animal species occupying sagebrush ecosystems are of conservation concern (Suring et al., 2005; Davies et al., 2011), and none are perhaps more emblematic than the greater sage-grouse (*Centrocercus urophasianus,* hereafter sage-grouse). Sage-grouse are a well-documented obligate species to sagebrush ecosystems whose declining populations and threats to critical habitat have prompted multiple listing assessments under the Endangered Species Act (hereafter, ESA) since the end of the twentieth century (U.S. Fish and Wildlife Service, 2015a). Concern over the loss of sagebrush ecosystems and the broad ecological and socio-economic consequences of listing sage-grouse under the ESA spurred the development of science-based plans that lie at the nexus of one of the largest conservation efforts in United States history (Department of Interior, 2015; U.S. Fish and Wildlife Service, 2015a).

These efforts provided a strong catalyst for bringing well-studied factors influencing resilience to disturbance and resistance to invasive species (hereafter, R&R) into an actionable framework to help guide management decisions (Pyke et al., 2015; Chambers et al., 2017; Crist et al., 2019). To a degree, this was borne of a growing body of collective research that pointed to a frequent lack of sagebrush restoration success and resultant ineffective use of limited economic resources (Davies et al., 2011; Arkle et al., 2014). What rangeland managers needed was a tractable and spatially explicit tool that could predict baseline conditions associated with active and passive restoration success. Leveraging well-quantified linkages between soil moisture availability, primary productivity, and susceptibility to invasion that correlate strongly with elevation and are modified by aspect and vegetation-altering disturbances, Chambers et al. (2014) developed the foundational framework for predicting edaphic conditions associated with

variation in R&R (in the sense of general resilience, **Table 1**) across sagebrush ecosystems. In brief, R&R is weakest at lower elevation sites characterized by Wyoming big sagebrush (*A. tridentata wyomingensis*) growing on warm and dry soil types, which are highly vulnerable to permanent transitions to novel and hysteretic ecosystem states driven by the loss of sagebrush, perennial grasses, and microbiotic soil crusts, and the subsequent domination of invasive annual grasses. In contrast, higher elevation sites characterized by mountain big sagebrush (*A. t. vaseyana*) and mountain shrubs growing on cool and moist soils where invasive annual grasses grow poorly have greater capacity for resilience. These concepts were made readily operational by classifying existing maps of soil climate that spanned the sagebrush biome into soil temperature and moisture regimes representing a gradient of underlying R&R properties (Maestas et al., 2016; Chambers et al., 2017). At its coarsest scale, soil regimes are aggregated into three categories that index R&R (low, moderate, and high), but use of temperature and moisture subclasses (Chambers et al., 2014, 2017, 2019a,b; Maestas et al., 2016) along with ecological site potential and collective responses to disturbance (Stringham et al., 2016) can facilitate applications with finer scale and grain (see section: Improving Estimates of Sagebrush Engineering and Spatial Resilience). This spatially explicit tool provided a foundation for triage of sagebrush management efforts across large spatial extents by identifying areas that would likely respond positively to active or passive restoration following disturbance vs. those that likely to respond poorly to restoration and hence prioritized for protection and management actions that enhance resilience (see section: Foundational Tools: Science Framework).

Threats to Resilience of Great Basin Sagebrush Ecosystems

Another important aspect of operationalizing resilience is understanding variation in biotic and abiotic stressors that provide energy for state changes across gradients of adaptive capacity that modify ecological resilience across large spatial extents (Gunderson, 2000; Scheffer et al., 2001; Folke et al., 2004). The Great Basin, comprising much of the western extent of the sagebrush biome, is larger than 80% of countries worldwide (Coates et al., 2016a), harbors > 45% sage-grouse leks rangewide (WAFWA, 2015), and includes an isolated Distinct Population Segment at the southwestern edge of the species' range (hereafter, Bi-State DPS) that has been evaluated separately for listing under the ESA (U S. Fish and Wildlife Service, 2015b). While sagebrush ecosystems and sage-grouse within the eastern portion of the range face threats arising directly from anthropogenic disturbances including cropland conversion and energy development (Doherty et al., 2016), managers of the iconic sagebrush ecosystems of the Great Basin face two primary biotic and abiotic stressors to R&R. The first is an accelerated cycle of wildfire driven by invasive annual grasses from Eurasia (hereafter, grass-fire cycle) and interactions with climatic conditions influencing loading and flammability of fuels, which is increasingly well-documented (Balch et al., 2013; Brooks et al., 2015; Coates et al., 2016a; Germino et al., 2016; Bradley et al., 2017; Pilliod et al., 2017a) and includes papers by Chambers et al. and Germino et al. in this special issue. Hence, we only briefly summarize the process here. This grass-fire cycle can be characterized by a non-analog positive feedback loop of fire, that kills most species of sagebrush, and is fueled by the invasion of winter annual grasses (mainly cheatgrass; *Bromus tectorum*) that can outcompete native perennial grasses by taking advantage of early fall and winter precipitation and high investment in seed production (Chambers et al., 2007). These grasses senesce by mid-late spring, much earlier than native perennials, and yield highly flammable fine fuels that spread fire to other stands of sagebrush that would otherwise not readily burn. The second is expansion of conifers, primarily single leaf pinyon (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*), into otherwise treeless and sagebrush dominated communities, and driven largely by changes in land-use practices, past wildfire suppression, and apparent changes in climate post-European settlement (Miller et al., 2005; Romme et al., 2009). While more of a press than pulse disturbance (Bender et al., 1984) in comparison to the grass-fire cycle, conifer expansion over time concomitantly reduces dominance of sagebrush and perennial grasses (Miller et al., 2005), provides greater inputs of large wood to fuel more intense wildfires (Strand et al., 2013), alters faunal community composition (Davies et al., 2011; Donnelly et al., 2017) and hydrological function (Kormos et al., 2017; Stringham et al., 2018). The grass-fire cycle and conifer expansion collectively reduce general and ecological resilience through overall degradation of sagebrush ecosystem processes and excess fuel loading that increase wildfire probability, and spatial resilience (**Table 1**) through often hysteretic transitions to large grass or woodland dominated states that fragment otherwise continuous sagebrush.

Adding Sage-Grouse Metrics to Resilience Models for Sagebrush Ecosystems

Ecosystem restoration focuses largely on interactions between plants and soils given that they are primary determinants of productivity, yet failure to consider the response of fauna when planning and predicting restoration outcomes can be an obstacle against making resilience more operational (Perring et al., 2015). Lack of explicit attention to faunal response, particularly those at higher trophic levels, can stem from "field of dreams" concepts (Palmer et al., 1997; Sudduth et al., 2011; Perring et al., 2015) that assume both positive and rapid responses to restoration treatments providing habitat components necessary for life history demands. However, these treatments may not always yield resilient populations owing to spatial and temporal lags between reorganization of plant and soil feedbacks and corresponding demographic response of higher trophic taxa (Miller and Hobbs, 2007; Perring et al., 2015) (**Figure 1**). For example, lags can occur when population performance or generation times of higher trophic organisms progress too quickly relative to slower reorganization of plant and soil, or when changes to state factors such as climate and potential biota occur over large spatial extents or higher frequency such that spatial resilience is lowered

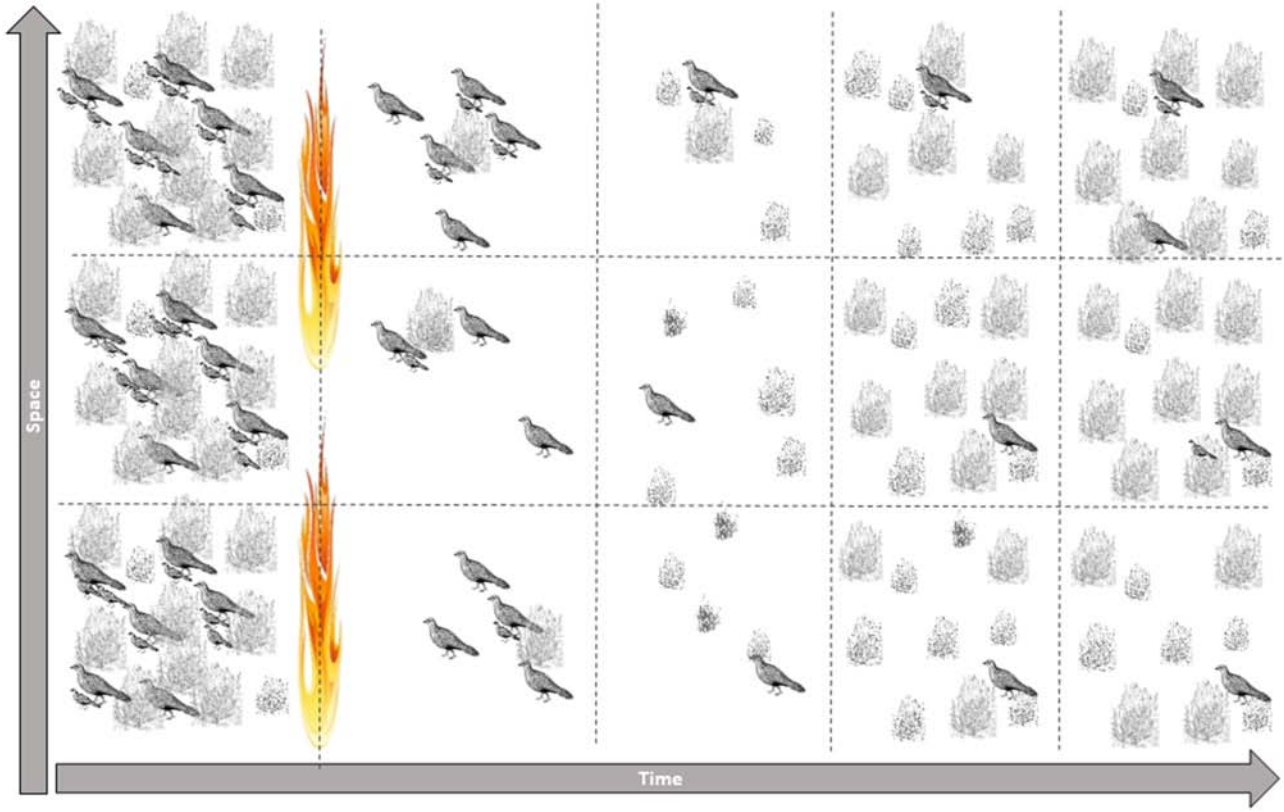

FIGURE 1 | Simple conceptual model illustrating asynchronies in engineering resilience between sage-grouse and sagebrush populations post-disturbance (e.g., wildfire). Even if sagebrush engineering resilience is high (as in high RandR habitats), sage-grouse population performance has lagged severely by the time sagebrush reaches pre-disturbance conditions. Reductions in survival and recruitment are illustrated by fewer hens with chicks; dashed lines represent time intervals; dashed horizontal lines represent closed populations. Spatial resilience is compromised when disturbance becomes widespread going from bottom to top.

by homogenization, even in ecosystems with relatively high resilience (Bestelmeyer et al., 2011). Consequently, if engineering resilience (i.e., rate of recovery to original condition, **Table 1**) is low, plant communities may eventually recover with or without active intervention over longer-time spans even after thresholds to disturbance have been surpassed, yet higher trophic organisms may show a more a hysteretic response (Bestelmeyer et al., 2011). Moreover, management actions intended to enhance ecosystem resilience to catastrophic disturbance and improve habitat quality for obligate species can create unintended ecological traps where animals select environmental cues that lower fitness (Battin, 2004).

It follows that while umbrella approaches focusing on single species have shortcomings (Andelman and Fagan, 2000), integration of metrics that account for measured responses of higher trophic taxa dependent on large and functional ecosystems should help facilitation of operational resilience (Suding, 2011; Perring et al., 2015). In our example, sage-grouse are well-recognized as an indicator species for the ecological integrity and conservation of sagebrush ecosystems at landscape scales, owing to the diverse array of community types used to meet life-history demands throughout their annual cycle (Rowland et al., 2006; Hanser and Knick, 2011; Runge et al., 2019). While not all ecosystem processes are covered completely under the umbrella of sage-grouse centric management approaches (Carlisle et al., 2018), evaluating resilience through additional lenses of sage-grouse habitat selection, population performance, and risks to persistence that are integrated with underlying sagebrush ecosystem R&R properties at multiple scales can help guide implementation and predict success of management actions (Chambers et al., 2017; Ricca et al., 2018). Herein, we: (1) summarize existing and new multi-scale tools, going from coarser to finer grain in terms of input data resolution and model complexity, as examples of integrating sage-grouse and sagebrush general and ecological resilience; and (2) describe general pathways forward for more explicitly integrating sage-grouse fitness and factors influencing variation in sagebrush R&R as metrics. In doing so, we aim to provide a more detailed operational definition of resilience for managers with quantifiable metrics that help guard against spatiotemporal mismatches owing to differences in engineering resilience between sagebrush ecosystem processes and sage-grouse population dynamics (Coates et al., 2016a), and how subsequent variation in feedbacks across space and time alter spatial resilience that contribute to sage-grouse population persistence across large spatial scales. We focus on tools aimed

at addressing threats to sagebrush ecosystems in the Great Basin in the western portion of sage-grouse range, but the concepts presented have broader applications rangewide. Our examples are based largely on published model frameworks, so we direct interested readers to consult referenced papers herein for more information regarding specific methods and validations.

FOUNDATIONAL TOOLS: SCIENCE FRAMEWORK

The Science Framework (Chambers et al., 2017; hereafter, Framework) serves as a solid baseline example for multi-scale integration of sagebrush ecosystem R&R concepts with ecological and management attributes associated with an indicator species represented by greater sage-grouse. Chambers et al. (2017, 2019b) provides a detailed summarization of the Framework and associated applications. Hence, a brief summary follows since it provides much of the conceptual basis of finer scale tools we describe next. A key element of the Framework at broad-to-mid scales is the spatially explicit intersection of data layers describing: (1) general resilience in sagebrush ecosystem R&R based on variation in soil temperature and moisture regimes described heretofore; and (2) a composite sage-grouse population index derived from lek-based models of sage-grouse breeding habitat probability and population abundance (Doherty et al., 2016). Importantly, incorporation of the sage-grouse population index represents an improvement over coarser-resolution available metrics such as percentages of sagebrush cover (Knick et al., 2013) or Priority Areas for Conservation (PACs, U.S. Fish and Wildlife Service, 2013) because it more directly accounts for habitat features selected by breeding sage-grouse in areas with abundant populations as determined by counts of sage-grouse at traditional breeding leks that are widely used to assess sage-grouse population trends (WAFWA, 2015). This property builds on the hierarchical approach of Coates et al. (2016b, 2019), which facilitates more precise prioritization of highly suitable habitats where sage-grouse are known to occur, while still accounting for unoccupied habitats of varying quality that may provide connectivity or other non-breeding life history needs. The binning of sagebrush R&R and sage-grouse population index layers into 3 respective classes each (i.e., high, moderate, and low) yields a 3 x 3 "sage-grouse habitat resilience and resistance matrix" that provides a highly tractable means for triaging management decisions relative to primary disturbance threats (e.g., conifer expansion, wildfire, invasive species) transcending broad to mid to local spatial scales across the species range (Chambers et al., 2016, 2017, 2019a,b). For example, reduction of conifer expansion in areas where shrub and herbaceous understories remain intact (i.e., Phase I or Phase II; Miller et al., 2005) can be aimed toward treatment of sites with underlying moderate to high R&R that are likely to support breeding sage-grouse. Wildfire prevention and suppression efforts are generally inversely related to R&R, and the strongest targeting occurs in high value areas characterized by low R&R that have high probabilities of breeding sage-grouse, where subsequent restoration efforts would have low chances of success. Moreover, the Framework facilitates ready inclusion of other spatially-explicit layers depicting relative risks of threats such as wildfire (Short et al., 2016), annual grass invasion (Boyte et al., 2019), and changing bioclimatic envelopes across different ecological gradients (e.g., Sage-Grouse Management Zones, Stiver et al., 2015). It can also readily adopt more complex models describing sagebrush ecosystem R&R, sage-grouse habitat selection and links to population performance, and disturbance threats at finer scale and grain; all of which aid effective targeting of management efforts to enhance operationalize resilience.

EXAMPLES OF INCREASING THE UTILITY OF SAGE-GROUSE METRICS TO OPERATIONALIZE RESILIENCE ACROSS SPATIAL SCALES

Sage-Grouse Population Response to Sagebrush R&R-Based Recovery Models

Despite prolific seed production, other functional traits of sagebrush species dominating the Great Basin (e.g., mountain big, Wyoming big, black, and low) such as fire-induced mortality, slow-growth rates, lack of biotic and abiotic dispersal mechanisms, and high seed and seedling mortality (Pyke, 2011; Knutson et al., 2014; Schlaepfer et al., 2014; Shriver et al., 2019) hinder multiple types of resilience in the face of altered or novel disturbances, which includes the grass-fire cycle. Ecological and spatial resilience has been stressed by an increase in fire size, recurrence rates, and rotation intervals over at least the past 30 years (Brooks et al., 2015), which collectively provide more sustained energy to push heterogenous sagebrush communities into homogeneous cheatgrass-dominated states across large extents, particularly those with soil climates associated with low R&R that dominate (i.e., comprise over 50%) the Great Basin (Maestas et al., 2016). Both general and engineering resilience is influenced in part by the R&R gradient (Chambers et al., 2014), whereby differences in plant-available soil nutrients and moisture coupled with adaptive species traits drive variation in sagebrush growth rates and resistance to invasion following disturbances such as wildfire. Subsequently, spatial resilience is influenced by ecosystem responses to active and passive management that vary with R&R.

While building upon the basic premise of the Framework as it developed, Coates et al. (2016a) formulated a predictive and spatially explicit model that accounted for variation in these types of resilience following wildfire relative to underlying R&R conditions and ecological needs of sage-grouse, and related the output to demographic responses of sage-grouse across the entire Great Basin over 30 years. In brief, annual fire perimeters and severity indices (>1) obtained from the Monitoring Trends in Burn Severity database (Eidenshink et al., 2007) yielded spatially explicit data for both fire size and frequency of fire recurrence (i.e., reburning of previously burned area). These data were intersected with the soil-climate based R&R layer, and annual sagebrush recovery rates derived from previously published studies were assigned to R&R index classes. Relatively

fast recoveries of 9 and 15 years were assigned to high and moderate R&R, respectively, and times were reset if fire recurred prior to recovery. In contrast, fire in low R&R were treated as permanent burn scars assumed to undergo a state-transition to cheatgrass. Importantly, engineering resilience post-fire was measured in terms of the amount to time necessary to provide a minimum of 20% sagebrush cover required for nesting sage-grouse. Sage-grouse population growth is sensitive to variation in nest survival (Taylor et al., 2012), and nest-survival is strongly tied to adequacy of concealment cover provided by sagebrush and other shrubs (Coates et al., 2017a). Sage-grouse also exhibit strong nest-site fidelity and do not readily vacate burned nesting habitat (Foster et al., 2019). Thus, the product of the model was an estimate of cumulative burn area (CBA) that accounted for chronic, rather than acute, wildfire effects on sage-grouse habitat needs during critical life-history periods relative to sagebrush recovery times that vary in relation to underlying R&R and fire recurrence rates. The amount of CBA has increased markedly over the last 30 years, with over 64,000 km^2 affected as of 2016 (**Figure 2**). Moreover, even relatively rapid post-fire recovery of sagebrush to minimum thresholds of nesting cover in moderate and high R&R likely were not fast enough to overcome asynchronies with sage-grouse habitat needs, and further explained chronic effects of widespread wildfire on sage-grouse population growth (**Figure 1**). It also provided a powerful mechanism for explaining long-term declines of sage-grouse across the Great Basin, which simulated drought conditions by negating normally positive periods of population growth during infrequent years of above-average precipitation, and forecasting significant sage-grouse population declines through ∼2040 even in habitats associated with high and moderate R&R if current rates of CBA remain unabated (Coates et al., 2016a). Moreover, the loss of spatial heterogeneity due to conversion of large swaths of burned sagebrush in low R&R areas, which dominate much of the Great Basin, to homogeneous stands of annual grass contributes to reduced spatial resilience and concomitant declines of sage-grouse with increasing CBA (**Figure 2**).

Refining Mid-Scale Spatial Intersections

A key component of the Framework is prioritization of management actions to prevent disturbance or identify best pathways for restoration following disturbance given underlying R&R and focal species (such as sage-grouse) needs at hierarchical broad, mid, and local scales. We provide three examples illustrating how finer resolution models depicting sage-grouse centric metrics can be integrated with R&R using the general geospatial overlay method of the Framework to address threats and prioritize management decisions at mid-scales (e.g., Great Basin, Bi-State DPS) stemming from wildfire and conifer expansion in a categorical fashion.

For our first example, we used a sage-grouse concentration area (hereafter; SGCA) geospatial layer modeled by Coates et al. (2016a) with the aim of identifying where wildfire management could be most beneficial to sage-grouse across the Great Basin. The SGCA was modeled as continuous surface using Doherty's et al. (2016) population index later integrated into the Framework, and then a threshold model was fit to identify where an increase in population index values no longer contributed to disproportionate population size relative to added habitat area. Binning the population index to this value (75%) identified areas that comprised < 10% of the Great Basin but harbored nearly 90% of sage-grouse populations. Subsequent simulation modeling indicated that reducing the rate of cumulative burn area by 75% in SGCAs could halt declining rates of sage-grouse population growth (Coates et al., 2016a); hence, the SGCAs layer is ideal for use in geospatial exercises for operationalizing resilience to wildfire that follow. Spatially explicit recommendations for highest prioritization of wildfire management actions are then determined by intersecting burn probability (Short et al., 2016), CBA, SGCA, and R&R geospatial layers (**Figure 3**). Our overall prioritization scheme is similar to that described for the Framework (Chambers et al., 2016, 2017), but varies with respect to identification of finer scale SGCAs and past fire history that key in on sage-grouse centric metrics and estimates of sagebrush engineering resilience.

Wildfire prevention areas are identified by intersecting the burn probability layer with the SGCA and R&R layers (**Figure 3A**). Priority for highest prevention can be placed in SGCAs likely to burn with low, followed by moderate, R&R. SGCAs with low R&R that are unlikely to burn can be afforded relatively less priority for prevention owing to limited fuel availability in these areas. Management actions such as conifer removal, targeted grazing, and strategic placement of fuel breaks for fuels reduction and staging areas for initial wildfire attack can be used to enhance prevention and resiliency to wildfire (Chambers et al., 2017, 2019b) in these priority areas. Once a fire ignites, spatial priorities for suppression and initial attack can be identified by intersecting the SGCA by R&R layer with CBA layer modified to illustrate recovered vs. non-recovered burned areas that as identified all past MTBS pixels with severity indices > 1 from the most recent annual CBA layer (**Figure 3B**). Highest priorities can be placed on SGCAs with low R&R that had not burned previously given low chances of active or passive restoration success and very low engineering resilience (Chambers et al., 2014, 2017). Subsequent high priorities can be placed in SGCAs with moderate and high R&R that had burned previously but recovered subsequently, followed closely by unburned SGCAs with moderate R&R. When prevention and suppression efforts fail, restoration resources can be expended in SGCA's with high and moderate R&R with recovered CBA, followed by the same areas that had not burned, given high chances of restoration success (**Figure 3C**). The rationale of prioritizing recovered CBA areas over previously unburned areas for suppression and restoration is predicated on efforts to reduce fire recurrence rates, and protection of SGCAs (and possible restoration investments) that likely now provide some minimal habitat requirements for sage-grouse after many years of sagebrush recovery and sage-grouse generations. Recovery processes can be further dissected by identifying burned high and moderate R&R pixels that have recovered vs. those in the process of recovery (**Figure 4**), and prioritizing SGCAs based on proportions of recovered CBA, recovering CBA, and unburned pixels. Prioritization rubrics can also be modified in instances, for example, where large unburned SGCAs are juxtaposed to smaller

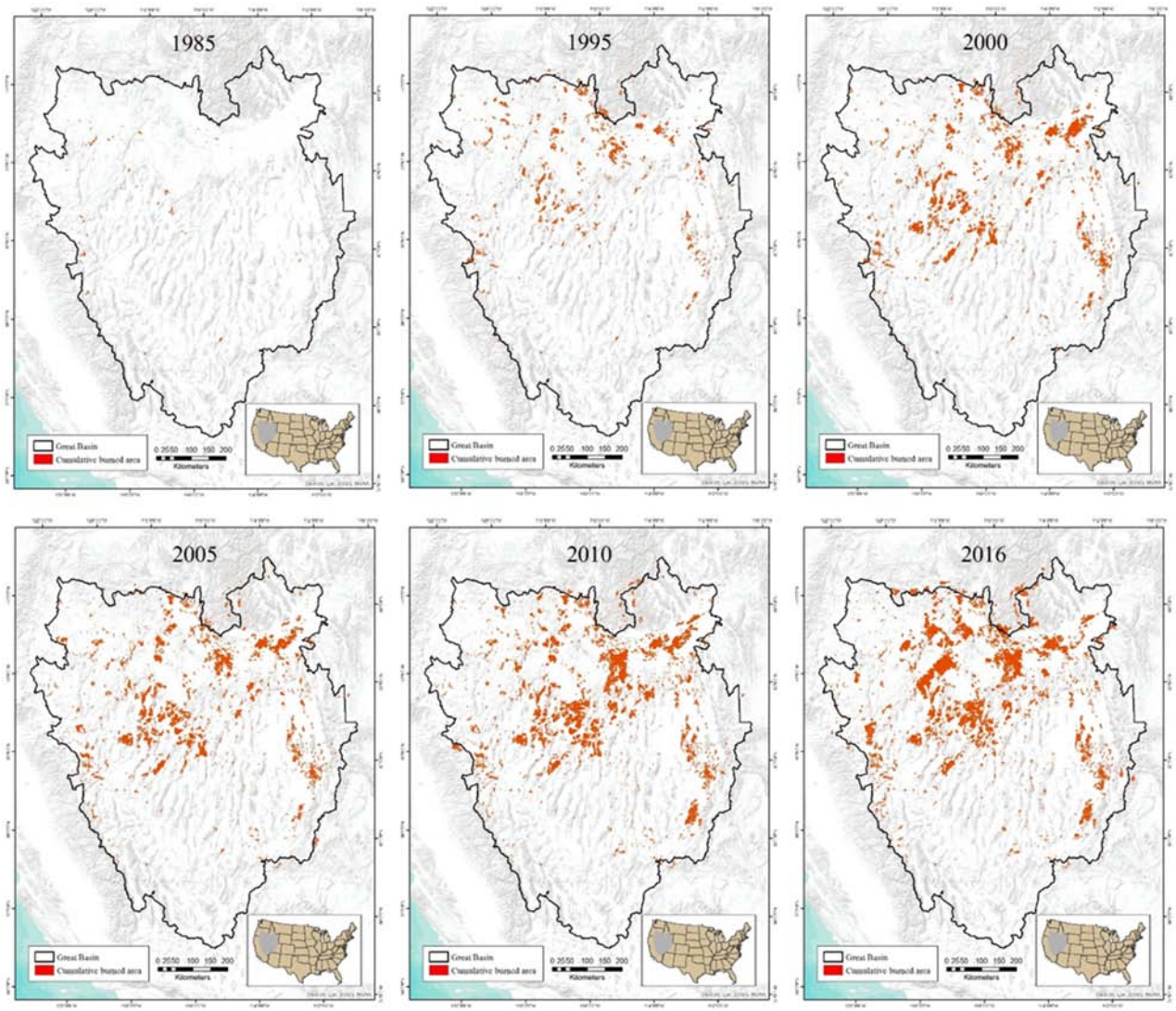

FIGURE 2 | Time series depiction of cumulative burn area (CBA) at 5–6-year intervals from 1985 to 2016 modeled with RandR-based recovery rules from Coates et al. (2016a).

SGCAs with recovered CBA (**Figure 4**), or in burned SGCAs with low R&R where active restoration efforts show signs of success (e.g., Germino et al., 2018).

Our second example builds upon the first, whereby we exchange the lek-based SGCA model at the ecoregion (i.e., Great Basin) extent with a telemetry- and lek-based model at the extent of Nevada and northeastern California to illustrate how inclusion of more localized models, where available, can provide finer resolution mapping of resilience-based management scenarios (**Figure 5**). For the latter case, habitat attributes disproportionately associated with leks relative to the random distribution of the same attributes provide more generalized models of habitat selection and hubs of population distribution because overall seasonal use patterns (particularly nesting) of non-migratory sage-grouse in the Great Basin are largely concentrated in diverse habitats within 5–8 km of leks (Coates et al., 2013; Manier et al., 2014). However, telemetry-based models can better account for specific resources selected differently among seasons by individual grouse to fulfill specific life-history needs such as nesting, brood rearing, overwintering, and movement corridors (Chambers et al., 2017). Compared to the SGCA-based overlay, a composite index derived by intersecting spatially explicit models of: (1) habitat selection informed by >44,000 locations from >1,700 telemetered sage-grouse that explicitly account for seasonal and regional climatic variation; and (2) a lek-based probabilistic index of abundance and space use (Coates et al., 2019) can provide finer scale depictions of predicted suitable habitat in areas likely occupied by sage-grouse (**Figure 5**). Subsequent intersections with R&R and recovered and non-recovered CBA layer using the same

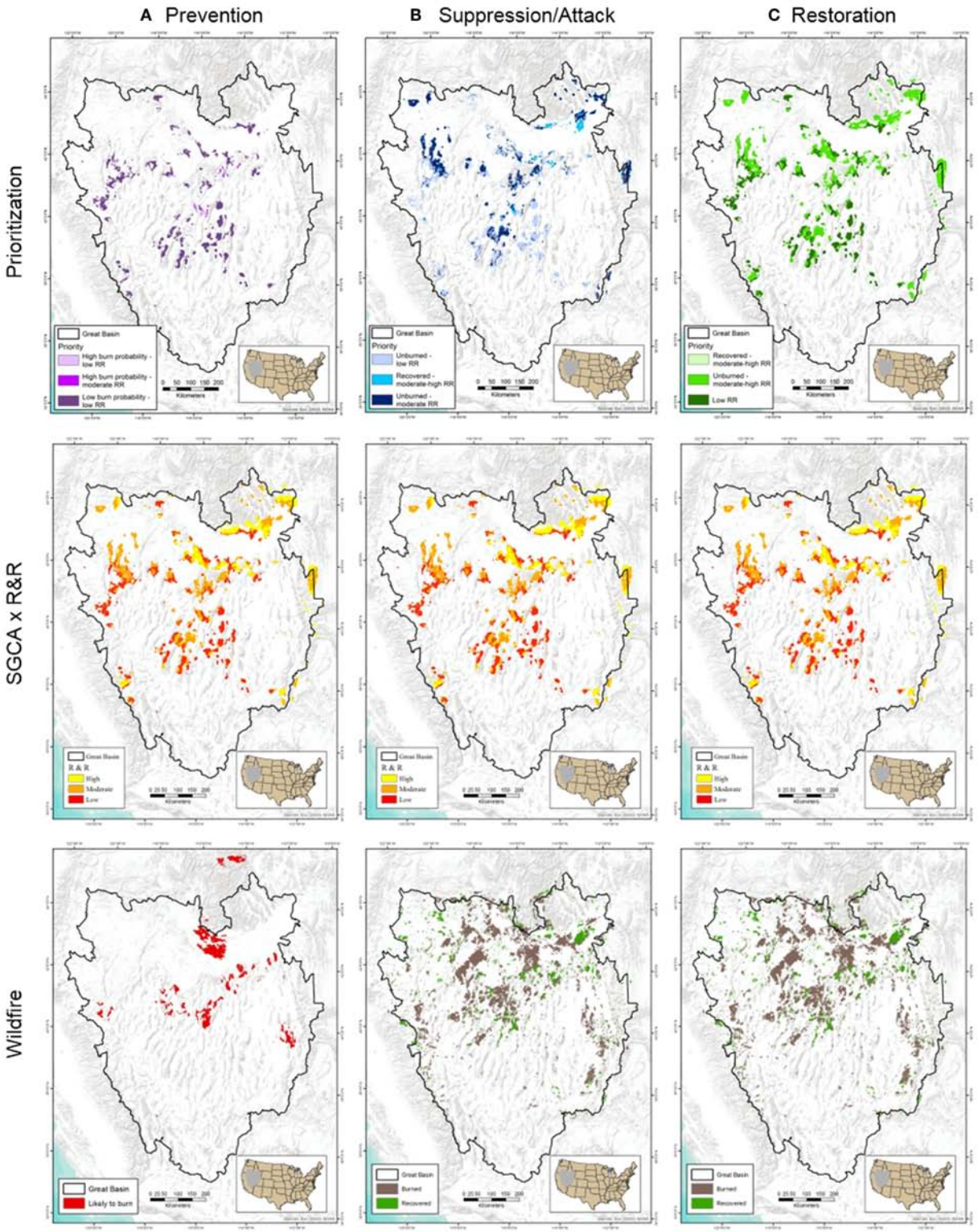

FIGURE 3 | Example spatially explicit strategies for prioritizing wildfire management in the Great Basin based on geospatial intersections of fire probability (Short et al., 2016), wildfire impacted areas (Coates et al., 2016a), soil regime-based resilience and resistance indices (RandR, Maestas et al., 2016), and sage-grouse concentration areas (SGCA, Coates et al., 2016a). The top row represents example prioritization for wildfire prevention **(A)**, suppression and initial attack **(B)**, and restoration **(C)** given results of spatial intersections (lower row) for fire probability (left column) or cumulative (or recovered) burn area (middle and right column), and SGCA x RandR (middle row). Prioritizations are ranked in descending order.

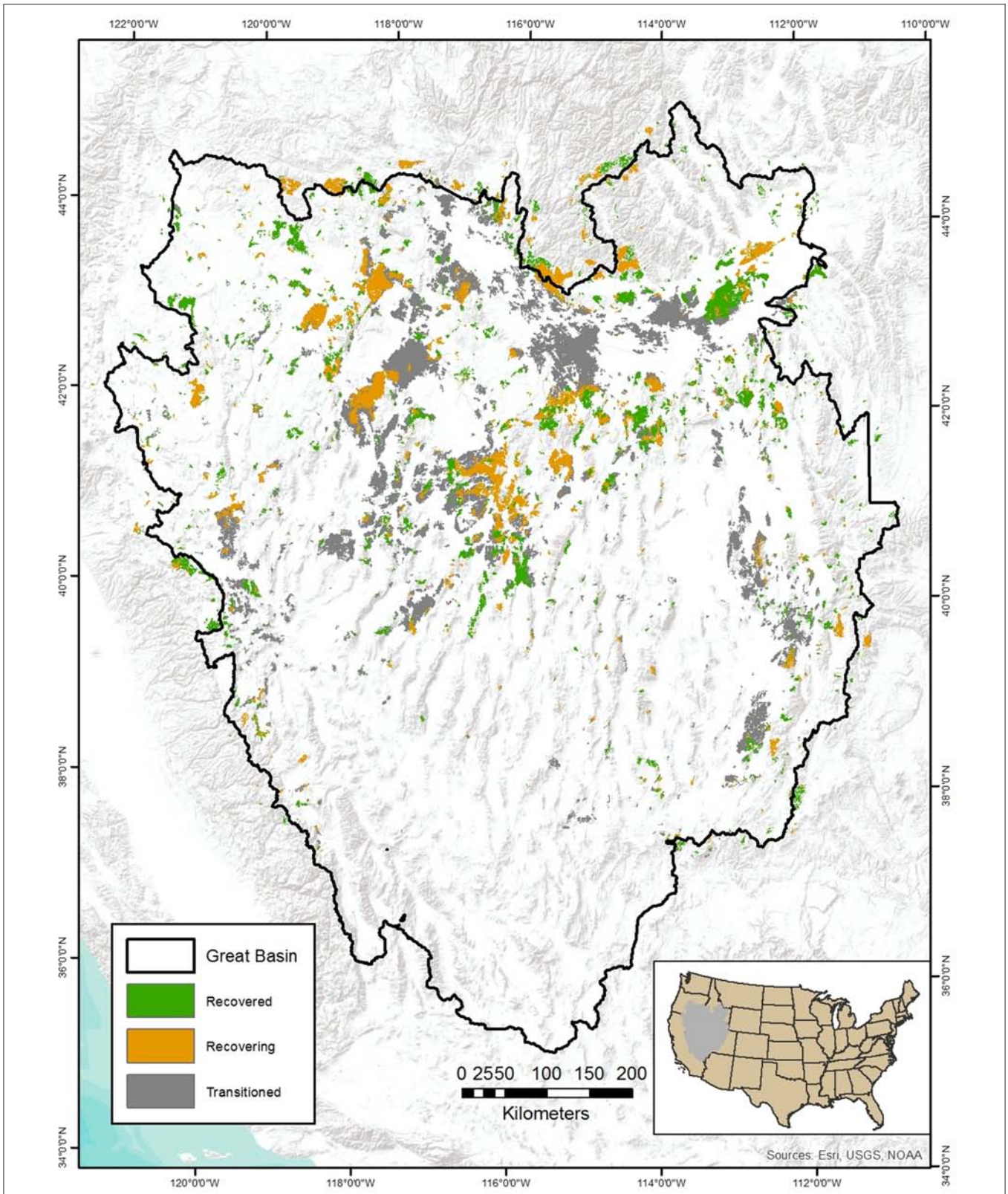

FIGURE 4 | Alternative layer for depicting wildfire impacted areas in **Figure 3** derived from geospatial intersections of high and moderate RandR areas with modeled complete or in-progress post-fire recovery, and areas of low RandR with modeled state-transition to annual grass using rules from Coates et al. (2016a).

rules in **Figure 3** for prioritization of wildfire prevention, suppression, and restoration can identify finer delineations for management actions such as fuel break and staging areas, tiered protection of continuous vs. fragmented habitat, and more targeted restoration efforts.

Our third example illustrates how multi-scale areas for conifer removal can be prioritized by using categories derived from models that link sage-grouse habitat selection and concomitant impacts on survival to probabilities of conifer encounter and underlying R&R. Management efforts aimed at treatment of conifers expanding into otherwise treeless shrubland in the Great Basin through thinning or complete removal have accelerated greatly over the last decade (Severson et al., 2017a; Ernst-Brock et al., 2019). In addition to well-quantified effects of conifer expansion on sagebrush structure and function (Miller et al., 2005), these efforts have arisen from an increasing body of work quantifying how conifer expansion reduces sage-grouse population performance through decreased lek persistence (Baruch-Mordo et al., 2013), nest and brood survival (Sandford et al., 2017), annual survival (Coates et al., 2017b), and altered movement rates (Prochazka et al., 2017). While dense stands of continuous conifer woodland with depauperate understories (Phase III expansion, Miller et al., 2005) can be targeted for fuels reduction (Chambers et al., 2017), treatments for the benefit of sage-grouse populations are more commonly aimed at sparsely distributed trees in areas with dominant and intact shrub and herbaceous understories (Phase I), or to a lesser degree, in areas with higher conifer density becoming co-dominant with understories (Phase II). The Framework also suggests targeting of treatments in areas with high to moderate R&R to increase sage-grouse habitat selection and connectivity, as well as resilience to wildfire by reducing loads of heavy woody fuel (Chambers et al., 2017).

Restoration of habitat to fulfill life-history requirements for sage-grouse is readily accomplished in Phase I (and to a lesser extent, Phase II) owing to the need to remove relatively few trees and having an intact shrub and herbaceous component often requiring minimal reestablishment (but see Roundy et al., 2014). Rapid increases in cover of herbaceous vegetation can also ensue rapidly after treatment (Severson et al., 2017a), which correlate with increases in post-treatment population growth for sage-grouse (Severson et al., 2017b). Nevertheless, untreated Phase I encroached sagebrush can provide attractive resources to sage-grouse in terms of ample cover of shrubs and herbaceous vegetation. It follows that at the level of the individual, some sage-grouse demonstrate selection for areas of Phase I expansion, and likely do not perceive threats from low density trees contributing to increased mortality risk from raptors that perch and nest on trees (Coates et al., 2017b). These individual choices had significant fitness implications, whereby sage-grouse that demonstrated complete avoidance of Phase I had 20% higher survival probabilities compared to those individuals who demonstrated no avoidance. Reductions in survival were also most pronounced in areas of high R&R that corresponded to productive and mesic sage-grouse habitat, which also likely attracts raptors. Such areas could be significant ecological traps to individual sage-grouse owing to a decoupling of environmental cues that lead to maladaptive selection (Battin, 2004). Population-level impacts and concomitant reductions in spatial resilience of both sagebrush ecosystems and sage-grouse populations can occur if such traps are widespread, as is likely the case throughout much of the Great Basin. Moreover, deleterious impacts on sage-grouse lek persistence (Baruch-Mordo et al., 2013) and annual survival (Coates et al., 2017b) have been quantified at a threshold of 1.5–2.0% canopy cover, so treatments in both Phases I and II could have unintended consequences for sage-grouse if remaining canopy cover exceeds that threshold.

Spatially explicit delineations of conifer-associated ecological traps could help guide managers when prioritizing pinyon-juniper treatment areas within sage-grouse habitat. Accordingly, we use a geospatial overlay approach similar to that described heretofore, focused on the Bi-State DPS where conifers have been identified as a primary threat to sage-grouse and removal treatments are a key conservation tool (U S. Fish and Wildlife Service, 2015b) (**Figure 6**). We utilized a high-resolution (1-m^2) map of conifer distribution and canopy cover derived from object-based image analyses of contemporary National Agricultural Imagery Program digital orthophoto quad tiles (Gustafson et al., 2017). Canopy cover classes (that index phases of encroachment) were estimated by calculating the proportion of mapped conifers within 900 m^2 pixels, where cover classes 1, 2, and 3 represented >0–10, >10–20, and >20% conifer canopy cover, respectively. Cover class 1 was intersected with areas of high R&R to demarcate possible ecological traps (as in Coates et al., 2017b) (**Figure 6A**), We then intersected the same SGCA layer used in the wildfire example with the high R&R by cover class 1 layer to provide broad-scale targets for conifer removal in areas of abundant sage-grouse populations occupying selected habitat as measured from a lek-based model (**Figure 6B**). As with the wildfire example, telemetry-based models can be substituted to provide finer grain resolution. Here, we use a categorized resource selection function intersected with an abundance and space use index developed for the DPS (Ricca et al., 2018) and extracted to the 85% isopleth, which depicts finer grain across a large spatial extent (**Figure 6C**). We repeated the same approach using cover class 2 to demarcate areas where incomplete thinning efforts could lead to unintended ecological traps (**Figures 6D–F**). This approach can be expanded to larger spatial extents covering much of the Great Basin (Gustafson et al., 2017), and intersections with moderate R&R classes performed to further triage removal priorities outside of possible ecological taps that occur in selected and occupied habitat, but have higher chances on annual grass invasion following treatment. Risks of treatment vs. improvement in sage-grouse habitat should be weighed particularly in dry sites with low perennial herbaceous cover following mechanical treatment (Roundy et al., 2014; Bybee et al., 2016).

Scaling-Down Mid-Scale Models to Better Inform Local Site Selection Processes

The mid-scale spatially explicit models of sage-grouse habitat selection and abundance distribution intersected with predicted responses to disturbance (e.g., conifer expansion and wildfire)

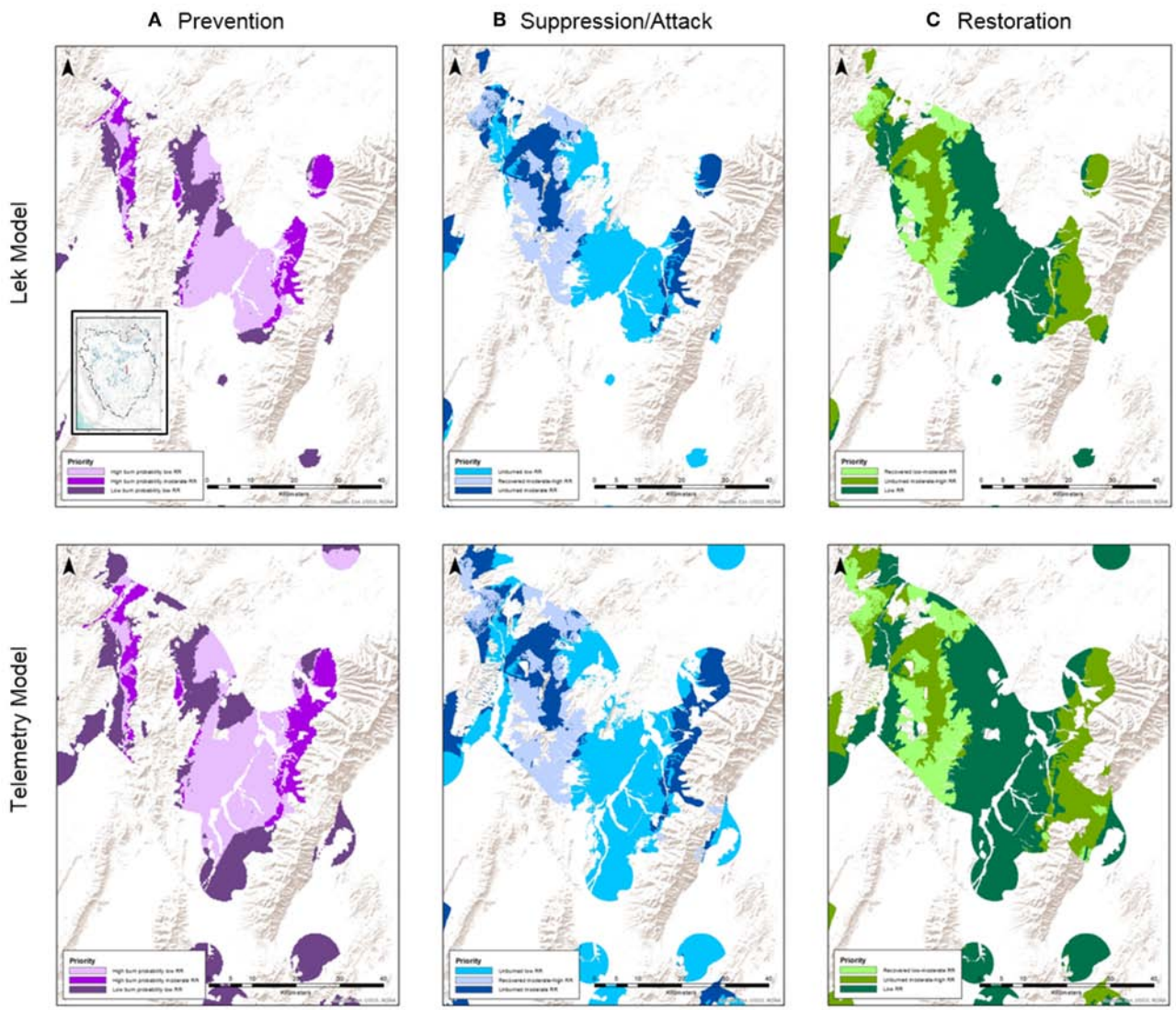

FIGURE 5 | Illustration of finer resolution prioritization of wildfire management strategies using geospatial overlay of **(Upper)** a lek-only based model of sage-grouse habitat and abundance using SGCAs vs. **(Bottom)** a telemetry-and lek-based model of sage-grouse habitat and abundance.

given underlying R&R properties help better identify areas for management across larger landscapes. Site-level implementation of management is also a key component of the Framework (Chambers et al., 2017; Crist et al., 2019), and direct application of mid-scale models may be too coarse in some cases to inform the most effective targeting of treatments given within site heterogeneity. In our examples, substantial variation in habitat selection within areas identified at the mid-scale can occur given inter-site differences in the availability of resources required by sage-grouse (Coates et al., 2019), and how that availability changes subsequent to disturbance and management carried out at a finer grain within the local scale. Here, we describe recently developed decision-support tools for conifer treatment and fire restoration that downscale mid-scale models, or leverage existing and extensive site-specific models, and apply simulated changes to land cover or habitat characteristics and concomitant quantified improvement in habitat quality to sage-grouse across candidate treatment sites while implicitly or explicitly considering underlying R&R. Such tools are also especially helpful when disturbance is widespread across mid-scale identified areas, but limited resources are available for uniform implementation of restoration treatments that are intensive and costly. In the process, spatial resilience can be enhanced by avoiding implementation of likely ineffective active management action within mid-scale identified areas.

Two recent studies (Reinhardt et al., 2017; Ricca et al., 2018) applied spatially explicit mid-scale models of sage-grouse resource selection across different life-stages to proposed or existing conifer removal treatment units identified by resource management agencies (e.g., Bureau of Land Management and

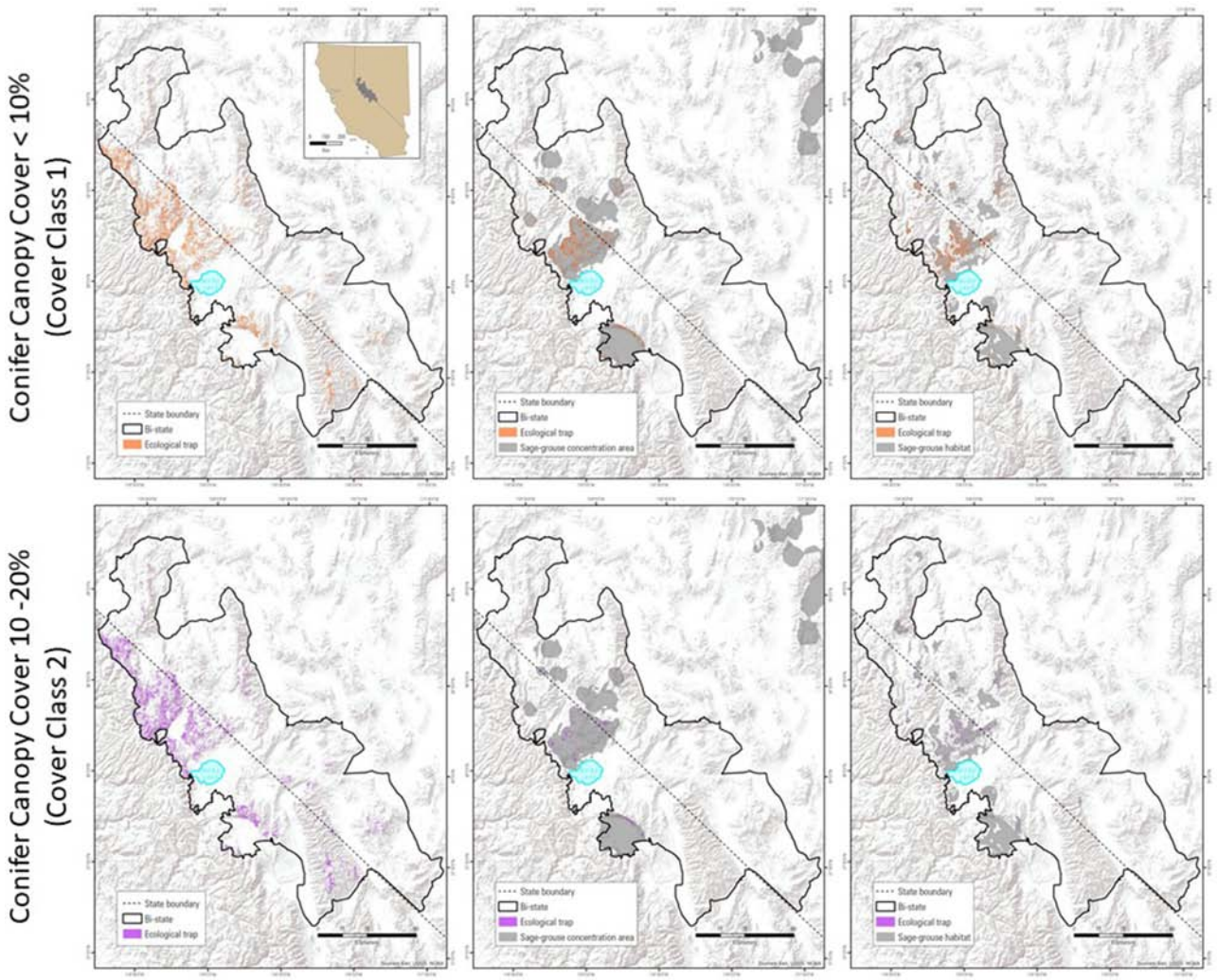

FIGURE 6 | Spatial overlay approach depicting the distribution of possible ecological traps to sage-grouse based on the intersection of cover-class 1 conifers with high RandR (upper row, **A**), and further delineated for management priority based on intersections with a lek-only based model of sage-grouse habitat and abundance using SGCAs **(B)**, and a telemetry-and lek-based model of sage-grouse habitat and abundance **(C)**. The lower row **(D–F)** represents ecological traps that could be created by thinning of cover-class 2 to cover-class 1 in high RandR areas.

Forest Service districts). Another recent study applied similar approaches to inform conifer removal for Gunnison's sage-grouse (*Centrocercus minimus*) but did not consider general R&R explicitly or implicitly (Doherty et al., 2018), so we excluded it from our review. In the Ricca et al. (2018) study, the goal was to rank candidate treatment units based on improvement of annual habitat selection following removal of Phase I conifer in the Bi-State DPS. In brief, a baseline resource selection function (RSF) describing features selected annually by sage-grouse of both sexes, including reproductive and non-reproductive females, status was calculated by contrasting existing land cover, topographic, and hydrologic attributes at multiple scales (e.g., moving windows) at used radio-telemetry locations compared to those at random locations. Conifer treatment and restoration of underlying shrub and herbaceous pixels were then simulated in a geographic information system (GIS) by: (1) removing conifer pixels, as measured from high-resolution mapping (Gustafson et al., 2017), comprising Phase I expansion (as indexed by cover class (1) within candidate treatment units, (2) returning understory pixels to their land cover type (e.g., big sagebrush, non-sagebrush shrub) without conifer overstory, and (3) re-running moving window analyses on land cover types and applying baseline RSF coefficients to the post-treatment landscape. Differences between pre- and post-treatments relativized RSF surfaces reflect per area increases in habitat selection, and multiplication by the lek-centric abundance and space-use index (AUI) account for spatial resilience by assigning higher rank to treatments in closer proximity to existing and sage-grouse populations (**Figure 7**). Final intersections with R&R allow inspection of

highly ranked treatments compared to relative risks of annual grass invasion following disturbance from removal. Notably, this approach indicated that the majority of ecological benefits can be comprised within just a few treatment units, treatments of identical cost can have substantially different benefits to sage-grouse, and focusing solely on treatments in high and moderate R&R can disqualify the highly ranked treatments that occur in low R&R, yet they can be treated with relative low risk using non-mechanical methods (Bybee et al., 2016).

In the Reinhardt et al. (2017) study, the goal was to prioritize conifer removal efforts at the mid-scale (southeastern Oregon) through a process that optimized improvements in breeding habitat, movements between breeding and brood-rearing habitats, and inter-PAC movements. That process used an ensemble of models describing lek distribution, breeding sage-grouse habitat selection (Doherty et al., 2016), conifer cover (Falkowski et al., 2017), mesic habitats for brood-rearing (Donnelly et al., 2016), landscape resistance (Knick et al., 2013), and R&R (Maestas et al., 2016). Costs were factored as combinations of conifer cover and R&R class (whereby high cover and low R&R have the highest risk). Prioritized sites were characterized by low canopy cover, high R&R, and abundant sage-grouse populations. Moreover, spatial resilience was enhanced ostensibly though selection of treatments that explicitly facilitated sage-grouse movement between seasonal reproductive habitats and larger-scale PACs. Model output had high concordance with treatments implemented closer to the start of the study period, which indicated the "best" sites may have already been treated and subsequent treated sites might yield limited returns. Importantly, both studies also stress that the models are meant to support the decision-making process at the local scale, and not supplant local knowledge. Still, use of simulated changes in sage-grouse habitat selection following conifer removal provides a useful tool for budget-limited managers to avoid implementation in areas with low benefit to sage-grouse and high risk of disturbance from intensive treatment.

The aforementioned studies contribute to a proliferation of research that explicitly incorporate general R&R into planning and prioritization at the local-scale within the context (implicitly or explicitly) of sage-grouse habitat requirements and distribution at mid-scales (e.g., Knutson et al., 2014; Pyke et al., 2015; Chambers et al., 2017, 2019b; Barnard et al., 2019). However, few have modeled specifically quantified changes in sage-grouse habitat selection post-restoration as a function of predicted land cover responses to underlying general resilience. The aforementioned Ricca et al. (2018) study provides an example for local-scale fire restoration that builds on the conifer removal example through simulation of land cover recovery on pixel by pixel basis in a GIS given: (1) burn severity driving likely land cover change, (2) decisions to conduct passive or active restoration, (3) pre-burn land cover composition, fuel type, and underlying R&R class, and (4) uncertainty in resistance to annual grass invasion for moderate and low RR classes (**Figure 8**). For example, while active or passive restoration in high R&R yielded return to sagebrush or original land cover type, active restoration in low R&R could yield mixed sagebrush establishment under a resistant outcome but annual grass monocultures under a non-resistant outcome. Application of pre-fire RSF coefficients describing sage-grouse habitat selection responses to simulated post-fire landscapes under the different restored and/or resistant outcomes allows ranking of average sage-grouse habitat selection post-fire among sets of candidate wildfire scars examined, as with the conifer example. However, wildfire often immediately impacts thousands of acres of sagebrush. Hence, spatial heterogeneity in post-fire sage-grouse habitat selection can also be visualized though these types of decision-support tools to provide managers better identification of targeted areas for restoration across larger burned landscapes. These areas could include isolated patches of readily restorable habitat likely to improve connectivity within juxtaposed larger patches of less-recoverable annual grass, and areas where restoration could lessen risks of annual grass invasion on peripheries of more resilient and resilient patches, thereby increasing suitability across larger patch sizes. Moreover, relatively simple rules for land cover conversion in the decision tree can be expanded with parameters describing the efficacy of different treatment types and variation in sagebrush or herbaceous recovery processes relative to finer-scale variation in underlying general resilience depicted in more specialized mapping layers, and (as with the conifer tools) can be expanded to mid-to-broad scales using generalizable models informed by sage-grouse habitat selection parameters measured across multiple sites (see section: Pathways for Improving Decision-Support Metrics).

Lastly, the above examples used mid-scale models to aid local decision support, but existing site-specific information on sage-grouse resource selection during critical life history periods prior to disturbance can also be leveraged opportunistically. The possibility for such data sets is increasingly likely, given the preponderance of sage-grouse studies employing intensive monitoring of marked sage-grouse to measure vital rates and spatial utilization across numerous sites in the fire-prone Great Basin, and more frequent and larger wildfires intersecting these sites. We provide an example of this scenario to help inform targeted restoration actions within the scar of a 1,277-km^2 megafire in northeastern California (Rush Fire) that occurred in 2012. This example is part of a larger and collaborative on-going project evaluating sage-grouse spatial and demographic responses to restoration treatments in expansively burned landscapes, and forth-coming papers will describe overall project objectives and information regarding specific sagebrush planting design, seedling survival, and sage-grouse responses. General statistical methods for this example are described in the **Supplementary Material Appendix I**. In brief, an extensive dataset of sage-grouse nesting locations (Davis et al., 2014) informed an RSF describing pre-fire nesting habitat selection. Using GIS simulation approach described heretofore, we: (1) converted burned pixels to bare-ground, (2) recalculated habitat availability with appropriate moving windows immediately following the fire, (3) applied pre-fire RSF coefficients to the post-fire landscape, (4) subtracted the post- from pre-RSF to describe relative loss of nesting habitat (i.e., $\Delta RSF_{nesting}$), and (5) categorize the $\Delta RSF_{nesting}$ by the 50th percentile to

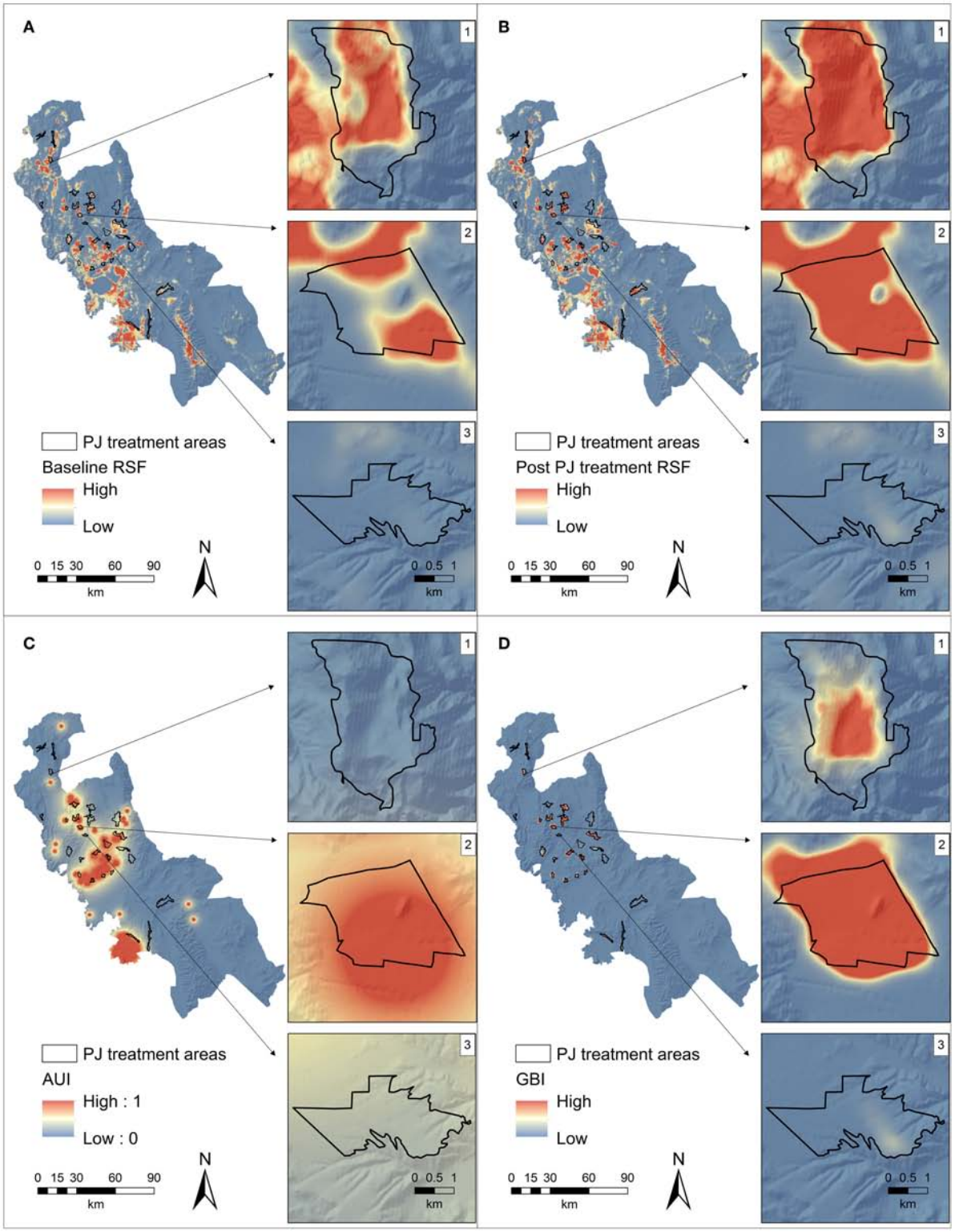

FIGURE 7 | Example spatially explicit illustration of effects of simulated conifer removal and subsequent change in ecological benefit to sage-grouse to prioritize treatments. Here, resource selection function (RSF) values between baseline **(A)** and post cover-class 1 pinyon-juniper removal **(B)** surfaces are subtracted, and then multiplied by an intersecting abundance and space use index (AUI) **(C)** to calculate a sage-grouse benefit index (GBI) **(D)**. Side panels illustrate how high GBI rankings can be driven by high RSF change and low AUI (1), high RSF change and high AUI (2), and low RSF change and moderate AUI (3). Used with permission from Ricca et al. (2018).

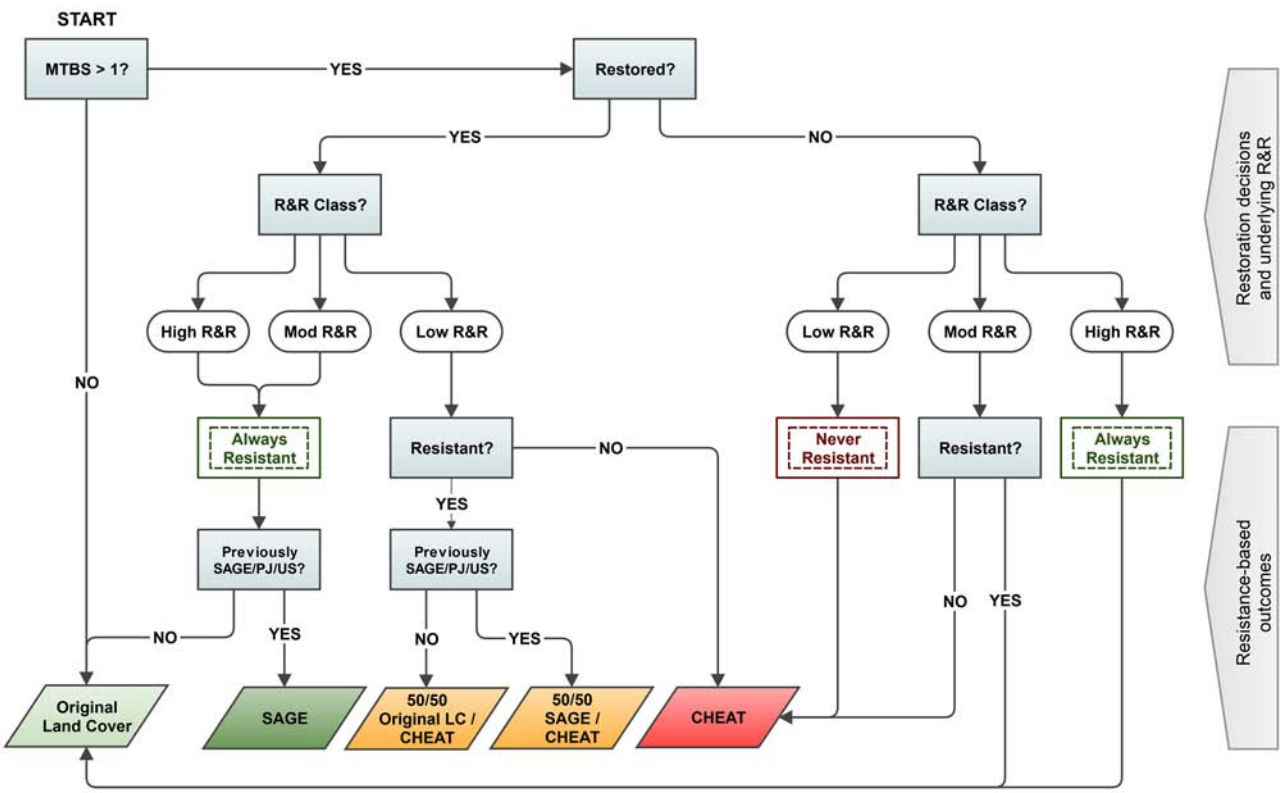

FIGURE 8 | Diagram of the decision model used to simulate outcomes of restoration decisions on land cover change (900 m^2) variation in burn-severity and resilience to disturbance and resistance to invasion (RandR) index classes. Local conditions may add uncertainty for resistance to cheatgrass invasion under some moderate and low RandR soil temperature and moisture regimes, so the model generates both Resistant and Not-Resistant outcomes in these cases following the decision to restore or not restore. Restored decisions assume active seeding or planting of sagebrush. Subsequent post-fire land cover surfaces can be used to model changes in sage-grouse habitat selection or suitability. Used with permission from Ricca et al. (2018).

identify core nesting loss (**Figures 8A–C**). Intersecting core nesting loss with R&R (**Figure 9D**) then facilitates more surgical targeting of intensive restoration in areas of the greatest loss of nesting habitat along a gradient of elevation and R&R and juxtaposed to existing leks (**Figures 8E–G**). Planting sagebrush seedlings in heterogeneously dense patches designed to provide minimum nesting cover within ∼3–4 years incorporates a resource island approach to restoration (Hulvey et al., 2017), which accounts for sage-grouse site fidelity to nesting sites despite disturbance, and can subsequently help ameliorate asynchronies in engineering resilience between recovering sage-grouse and sagebrush populations post-fire.

PATHWAYS FOR IMPROVING DECISION SUPPORT METRICS

The examples help bridge gaps in linking resilience concepts based on plant and soil processes driving ecosystem productivity with responses of higher trophic level and indicator species such as sage-grouse. A key to this process is identification of spatial relationships describing sage-grouse distribution and habitat selection with predicted sage-grouse and sagebrush ecosystem responses to disturbance and subsequent restoration efforts. Mid-scale examples focus on prioritization of active and passive actions using a geospatial overlay approach derived from the Framework. Telemetry-based models of habitat selection and high-resolution mapping of conifer canopy cover could be expanded to the broad-scale as soon as rangewide companion models are derived. Changes in land cover composition given underlying R&R using local scale models allow further quantification of spatial heterogeneity in improvement in sage-grouse habitat selection following disturbance and restoration, and those reorganized process can be scaled hierarchically to mid-and-broad scales (Perring et al., 2015) using generalizable models informed by datasets spanning multiple sites and years. Identification of temporal mismatches in engineering resilience between sage-grouse and sagebrush population dynamics impacts provides an explanation for the overall processes driving negative sage-grouse population growth with cumulative impacts of wildfire. Nevertheless, the decision support tools we described can be improved greatly through more explicit quantification of impacts on sage-grouse fitness and movement connectivity following disturbance and restoration under different scenarios of changing land cover composition, and by adding more complexity to sagebrush

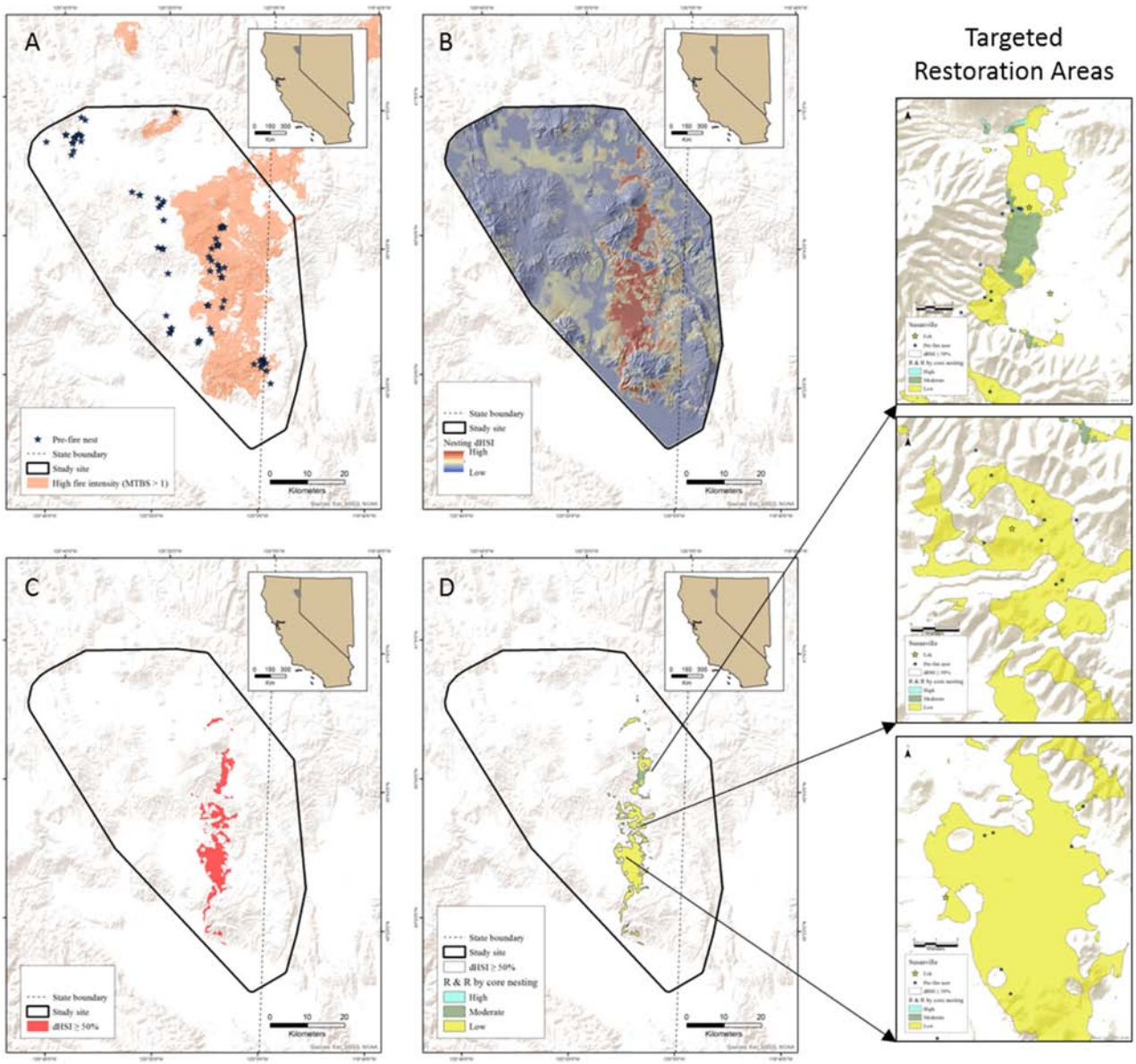

FIGURE 9 | Example of identifying areas for targeted restoration of sage-grouse nesting habitat affected by the Rush Fire in northeastern California. Pre-fire sage-grouse nest locations **(A)** inform a resource selection function of habitat loss post-fire **(B)**, which is categorized by the 50th percentile representing core loss **(C)** and intersected with RandR **(D)**.

recovery models to better reflect spatial heterogeneity in feedbacks driving resilience.

Incorporating Sage-Grouse Fitness Consequences

Analyses that quantify disproportionate use or avoidance (e.g., resource selection functions) are often used to infer suitability resource configurations for meeting life history needs. Yet, the true measure of suitability relates to differential fitness in terms increased survival and reproduction leading to population stability or growth (Hirzel and Le Lay, 2008; Gaillard et al., 2010). Inferences of suitability from selection can be confounded by existence of density-dependent source-sink dynamics (Matthiopoulos et al., 2015) and the aforementioned ecological traps, which are known to exist across sage-grouse populations (Aldridge and Boyce, 2007; Coates et al., 2017b; Heinrichs et al., 2018) but can be difficult to quantify due to modeling complexity and data limitations across broad spatiotemporal scales and finer grain. Recent advances in hierarchical modeling frameworks and computing power can help facilitate a shift from resource selection- to fitness-based metrics for use as ecological currency in decision support tools.

For example, significant advances have been made in spatially explicit estimation of population change (i.e., lambda) derived from demographic matrix or integrated population models that share information across multiple datasets and account for observation error (Chandler et al., 2018). Subsequent output can provide more refined geospatial overlays depicting areas with predicted population growth under both current and disturbance-induced conditions parametrized as multi-scale land cover covariates, which help identify specific habitats whose loss correlates with reductions in population growth and provide another measure for prioritization of prevention, suppression, and restoration efforts (e.g., **Figures 3–5**). Hierarchical Bayesian models also allow ready linkage of posterior parameter distributions describing resource selection during specific life-stages with those describing concomitant survival probabilities (Coates et al., 2017b). Such approaches were used recently in a generalizable mid-to-broad scale model that depicted source-sink dynamics in relation to habitat features and underlying coarse-scale R&R conditions influencing sage-grouse nest selection and survival across much of the Great Basin (O'Neil et al. unpublished manuscript). That study also determined that underlying R&R conditions mediated sage-grouse functional responses to habitat features (e.g., stronger selection for sagebrush in areas with low R&R), yet nest survival increased concomitantly with R&R. Similarly, individual-based models that simulate how demographic outcomes across an individual's life cycle are modulated by interactions with changing landscape features have been constructed to map source-sink dynamics on the northern periphery of sage-grouse range (Heinrichs et al., 2018). Spatially explicit depictions of how sage-grouse gene-flow at mid-to-broad scales is constricted once reductions in habitat suitability surpass thresholds indexing impermeability to movement that further inform estimates of meta-population persistence (Fedy et al., 2016; Row et al., 2018). Spatially explicit layers from such studies fit nicely in geospatial prioritization overlays, and changes in fitness landscapes following land cover change from disturbance or restoration as mediated by R&R can be estimated directly in a GIS using model-derived parameters. Moreover, fitness-based measures help better identify thresholds of resource loss (Standish et al., 2014; Chambers et al., 2019a) that tip populations from growth or stability to decline and provide a quantification of energy needed to surpass ecological resilience into undesired states.

Improving Estimates of Sagebrush Engineering and Spatial Resilience

The examples we described integrate sage-grouse metrics with coarse, 3-level indices of R&R (Maestas et al., 2016), which represented the first generation of spatially explicit estimates of general R&R in the original Framework (Chambers et al., 2017). These indices represent an aggregation of much finer soil temperature and subclasses that provided a highly tractable approach for managers faced with decision making at broad to local scales from spatial overlays and corresponding 3 x 3 decision matrices. Accordingly, they provided a useable and novel means for modeling sage-grouse population dynamics (Coates et al., 2016a) and habitat selection (Coates et al., 2016b; Ricca et al., 2018, other examples heretofore) as a function of resource availability following disturbance as mediated by underlying R&R. However, a strength of the Framework and subsequent approaches that follow is the ability to readily incorporate newly available information. Such information is now proliferating in the literature, and we provide general pathways for incorporation of new models of sagebrush population dynamics, state-transition, and general resilience to produce more refined predictors of engineering and spatial resilience.

First, coupling sage-grouse population growth models (e.g., Coates et al., 2016a) with better parameterized models of sagebrush population growth and corresponding estimates of cumulative burn area (CBA) should help ameliorate (or at least better identify and subsequently prioritize) mismatches in engineering resilience across spatial scales. For example, strong transient dynamics (i.e., where short term population trends following disturbance are decoupled from those resulting in undisturbed long-term trends) have been identified recently across seeded post-fire sagebrush populations across the western U.S., which arise due to altered population size structure post-disturbance and reduced survival and fecundity of seedlings compared to more robust and established plants (Shriver et al., 2019). The Shriver et al. (2019) study highlighted that while establishment is promoted during years of favorable wet and cool overwinter conditions, transient dynamics are often difficult to overcome due to low sagebrush density or outright failure in sites with predicted long-term sagebrush stability. Similarly, Requena-Mullor et al. (2019) demonstrated stronger effects of past local fire history (in terms of number and occurrence) compared to regional climate on big sagebrush occurrence and cover, while restoration only impacted occurrence and cover across the Great Basin. These results also further highlight the importance of conducting targeted restoration in areas with high reproductive value to breeding sage-grouse to help overcome differences in sage-grouse and sagebrush engineering resilience (**Figure 1**), such as the example we describe for the Rush Fire restoration (**Figure 9**). Using techniques such as seedling-based treatments that help bolster immediate survival probability and subsequently help overcome transient dynamics from seeded treatments, particularly if replicated across densely-planted patches that account for high first year seedling mortality (Brabec et al., 2015) could still provide cover for nesting sage-grouse in a short amount of time. Such efforts require substantial time and effort, which is another reason for a highly surgical approach.

Second, parameters from studies that explicitly model variation in sagebrush recovery processes as a function of underlying R&R can better inform predictions from state-transition models (e.g., Briske et al., 2008; Stringham et al., 2016; Chambers et al., 2017) and subsequent sage-grouse response. Similar to the studies described above, additional meta-analyses of space for time studies describing sagebrush recovery processes (e.g., Knutson et al., 2014; Barnard et al., 2019) following restoration (Pilliod and Welty, 2013; Pilliod et al., 2017b) in the context of spatially explicit R&R layers at coarse to fine scales (e.g., soil moisture and temperature sub-classes) would be especially useful; as would back-in-time approaches (Shi et al.,

2017) that leverage extensive time series of archived satellite data (e.g., Landsat) across expansive extents to classify changes in land cover at relatively high resolution (e.g., percentages of functional plant types with 900 m^2 pixels) (Xian et al., 2015) and then relate back to R&R in a similar fashion. For the latter case, Monroe et al. (2020) recently utilized a back-in-time approach to quantify factors influencing sagebrush recovery on reclaimed well-pads in Wyoming, and found that dynamic variables such as annual precipitation and temperature modified annual rates of change in cover (e.g., engineering resilience) based on more static state-variables such as soil type and topographic position describing general resilience. Specifically, growth rates increased more strongly following warm and wet conditions in higher elevation sites but declined with warmer conditions in lower elevation sites. Dynamic patterns in precipitation can also have strong, differential impacts on annual availability and drought resiliency of mesic resources across elevational and mid-scale ecoregional gradients (Donnelly et al., 2018). Models such as these that quantify modifications of static predictions of sagebrush engineering resilience by inter-annual variation in precipitation and temperature can further help parameterize decision-support tools for sage-grouse given that sage-grouse populations respond positively to pulses of above average precipitation at local- (Blomberg et al., 2012) and mid-scales (Coates et al., 2016a; Donnelly et al., 2018).

Third, soil-based geospatial layers describing layers general resilience can be broken down into finer levels of organization for subsequent use in predictive models of sagebrush recovery and state-transition, and then substituted in sage-grouse geospatial overlay or simulation analyses. For example, the aggregated 3-class R&R index of Maestas et al. (2016) can, and has been, deconstructed into finer subclasses of soil moisture and temperature regimes, with companion state-transition models nested within ecoregion and major land use area type across the eastern portion of sage-grouse range (Chambers et al., 2016). A similar framework has been developed for much of the Great Basin that aggregates local sites with different ecological potential, as governed by soil and climate conditions, into more manageable yet still fine-scale groupings based on shared predicted responses to disturbance and associated state-transitions also nested within major land use areas (i.e., DRGs, Stringham et al., 2016). Newly developed mid-scale spatially explicit models that leverage multi-decadal measures of plant-greenness with biophysical covariates (e.g., topographic position, soil organic matter, and available water capacity) to map disproportionate deviation of current vegetation composition and structure from estimated site-potential along elevational and disturbance gradients across the Great Basin represent a very powerful new tool (Rigge et al., 2019). Development of spatially explicit models depicting variation in soil macro and microbial biota, which also influence resistance to annual grass invasion (Belnap and Phillips, 2001; Bansal and Sheley, 2016), would allow novel incorporation of rather under-studied yet important soil process. Collectively, layers such as this help downscale coarser R&R predictions of potential community state-transitions following disturbance given finer-scale edaphic, topographic, and climatic conditions, and are better informed by parameters derived from empirical models described above. However, spatially explicit modeling of state-transitions is still in a nascent stage, largely due to difficulty in parameterizing complex processes and common reliance on information synthesized from the literature or expert opinion. While still very useful, practitioners who use these tools need to be cognizant that model output is determined largely by user-defined deterministic rules and requires independent validation (Requena-Mullor et al., 2019; Chambers et al., 2019b). Importantly, the conservation planning tools simulating changes in land cover given underlying R&R that we described, even with greater modeled complexity, also fall under this same caveat.

CONCLUSION

Model-based efforts toward operationalizing resilience in sagebrush ecosystems show significant impact. For example, a Web of Science search (model* and resilience and restoration) listed Briske et al. (2008) who first described incorporation of resilience into rangeland state-transition models, and Chambers et al. (2014) as described above, as the 9 and 10th most cited papers, respectively. Moreover, a key benefit of this impact, and subsequent unprecedented efforts toward the conservation of the imperiled sagebrush biome over the past decade, has been an increasing integration of foundational and novel ideas from the fields of ecosystem restoration, rangeland, and wildlife ecology. Here, we provided multiple examples using geospatial overlays and simulation approaches that demonstrated how multi-scale linkages of underlying general resilience with "sage-grouse centric" measures of population performance and resource availability. Results yield highly tractable decision-support tools for real-world managers that help increase interconnected ecological, engineering, and spatial resilience for both sage-grouse populations and sagebrush ecosystems. We note that while our examples focused on operationalizing resilience to conifer and wildfire, similar approaches could be applied to other disturbances such as energy and agricultural development and help guide grazing regimes for livestock and free-ranging equids given appropriate parameterization. We also recognize that the multiple and somewhat independent decision support tools presented could be confusing for managers in need of more comprehensive tools housed in a single, "one-stop-shopping" type of framework. Tools that differentially weight different desired outcomes through structured decision models (e.g., Martin et al., 2009) made spatially-explicit would help bridge this gap for managers. Lastly, we stress the need for structured long-term monitoring of focal species responses to validate predicted outcomes of restoration from these approaches (Suding, 2011). Sage-grouse are also a highly useful species to link plant and soil with higher trophic responses, yet the concepts and tools we described can be applied using other indicator species or assemblages of species, including those with different life-history strategies and resource needs that might not be covered always under the umbrella of sage-grouse (Carlisle et al., 2018).

DATA AVAILABILITY STATEMENT

Geospatial layers are available for download at the USGS ScienceBase website. Prioritization examples for wildfire and conifer management (**Figures 3**, **4**, **6**) are available at https://doi.org/10.5066/P960W8MD. Additional layers are available at https://doi.org/10.5066/F7G15ZRN, https://doi.org/10.5066/F7K35RRS, and https://doi.org/10.5066/F7TT4Q5S.

ETHICS STATEMENT

Sage-grouse marking efforts for the authors' field studies that generated data, in part, for this manuscript were vetted and approved by the USGS-Western Ecological Animal Use and Care Committee (USGS_ACUC-002).

AUTHOR CONTRIBUTIONS

PC and MR conceived the ideas and models described within that integrate sage-grouse and sagebrush R&R metrics. MR and PC wrote the manuscript and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00493/full#supplementary-material

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Resilience Concepts and Their Application to Coral Reefs

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The concept of resilience is long established across a wide-range of disciplines, but its evaluation in many ecosystems has been challenging due to the complexities involved in quantifying a somewhat abstract dynamical phenomenon. We develop a framework of resilience-related concepts and describe their methodological approaches. Seven broad approaches were identified under the three principle concepts of (1) ecological resilience (ecological resilience, precariousness and current attractor), (2) engineering resilience (short-term recovery rate and long-term reef performance), and (3) vulnerability (absolute and relative vulnerability) respectively. Using specific examples, we assess the strengths and limitations of each approach and their capacity to answer common management questions. The current synthesis provides new directions for resilience assessments to be incorporated into management decisions and has implications on the research agenda for advances in resilience assessments.

Keywords: management, recovery, resistance, assessment, framework

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INTRODUCTION

From its early use in physical sciences and ecology, the concept of resilience is now ubiquitous across natural and social sciences including psychology (Luthar et al., 2000), urban planning (Eraydin and Tasan-Kok, 2013), disaster management (Manyena, 2006), resource-dependent industries (Marshall, 2010), economics (Common and Perrings, 1992; Brand, 2009), and governance (Lebel et al., 2006). The concept has become increasingly malleable to fit different objectives and exhibits considerable variety in its application (Brand and Jax, 2007; Martin-Breen and Anderies, 2011; Davidson et al., 2016).

While quantification is necessary to operationalize the resilience of ecosystems, it has largely remained a conceptual phenomenon until recently. Feature issues published in the *Journal of Applied Ecology* (Angeler and Allen, 2016) and *Trends in Ecology and Evolution* (Hodgson et al., 2015) demonstrate ongoing dialogue to quantify resilience and the relevant key questions. How can resilience be operationalized using existing frameworks? What are the appropriate metrics to measure resilience in different ecosystems? Although recent studies advocate for generic indicators to achieve standardized quantification across systems, such as the measurement of resistance and recovery (Hodgson et al., 2015; Nimmo et al., 2015), general metrics may not be easy to measure across all systems, each with distinct system dynamics exhibiting different behaviors and governed by different processes and mechanisms (Dakos et al., 2015; Yeung and Richardson, 2015; Petraitis and Dudgeon, 2016).

Reviews of resilience have focused on quantification approaches across multiple ecosystems (Scheffer et al., 2015; Allen et al., 2016; Quinlan et al., 2016), drawing heavily on models of ecosystems including lakes (Carpenter et al., 1999), savannahs (Walker et al., 1981), and coral reefs. Although a number of reviews have considered the processes that drive resilience and its application to management (Bellwood et al., 2004; Hughes et al., 2005; Nyström et al., 2008; Mumby et al., 2014a), a critical review of approaches is lacking.

Here, we synthesize progress on the measurement of resilience on coral reefs and identify several novel, additional concepts that might have utility. We begin with a brief historical perspective of reef resilience concepts and provide a framework to categorize approaches. We then assess the strengths and weaknesses of various approaches and identify appropriate management questions. Finally we discuss new directions for resilience assessments, with an emphasis on improving the most common metrics-based approaches.

HISTORICAL PERSPECTIVE OF CORAL REEF RESILIENCE SCIENCE

In the late 1960s, ecologists began to study the ability of ecosystems to exhibit alternative community states, each of which appeared to be stable over time, occurred in the same environment, and was fairly resistant to disturbance (Lewontin, 1969; Holling, 1973). The term given to this phenomenon was "ecological resilience" and ecosystems were said to be attracted to alternative equilibrial states (Holling, 1973). Perhaps the first evidence that coral reefs might exhibit multiple "stable" states was the discovery of a patch of the relatively unpalatable macroalga, *Asparogopsis taxiformis*, after a ship grounding and pollution event on the outer Great Barrier Reef (GBR, Hatcher, 1984). Hatcher hypothesized that pollutants had provided an opportunity for the algae to bloom and once established, algae persisted by reaching a size escape from herbivory. Thus, different communities could emerge at different environmental levels but the system was likely stable even when nutrients returned to pre-disturbance levels (though this was not verified).

Nearly a decade later, the prospect of major shifts in coral community structure was revisited in a special issue of the journal American Zoologist. Done (1992) coined the term "phase shift" to describe a conspicuous change in community structure, referring to a drastic change from coral to macroalgal dominance. The term phase shift is symptomatic with no explicit connotation of stability (Petraitis and Dudgeon, 2004), and might involve alternative community states that become resistant to change owing to ecological feedbacks, or simply represent a reversible monotonic response of an ecosystem to a changing environment. In the same special issue of the journal, Knowlton (1992) published the first critical examination of mechanisms that might drive the existence of multiple alternative states on coral reefs. She mooted the idea that depleted herbivory could influence the competitive outcomes between corals and macroalgae and stabilize algal-dominated states. McManus and Polsenberg (2004) then proposed a conceptual model of key factors involved in reef phase shifts. To develop and reinforce the existence of multiple alternative states in reefs, Mumby and colleagues (Mumby et al., 2007) used a spatially-explicit and field-validated model of Caribbean coral communities. They proposed that the emergence of alternative states was a recent phenomenon in the Caribbean because reefs are not predicted to shift and lock when fast-growing acroporids or herbivory by sea urchins are returned to the ecosystem (Mumby et al., 2013b) yet both had been devastated from disease in the 1980s.

Although the existence of alternative stable states is a nuanced and by no means a universal phenomenon (Fung et al., 2011; Mumby et al., 2013a), the fact that some reefs have low resilience is beyond question. As more cases of reef decline and recovery were investigated, it became clear that reefs are profoundly dynamic systems that react and recover differently to perturbations, and that resilience cannot be taken for granted (Pearson, 1981; Brown and Suharsono, 1990; Ginsburg, 1993; Hughes and Connell, 1999; Bellwood et al., 2004; Graham et al., 2015). Moreover, Connell (1997) reviewed global patterns of reef recovery and found striking variability across the Pacific and the Caribbean; a pattern that persists today (Roff and Mumby, 2012).

With growing awareness that the health of some reefs was experiencing persistent decline in the 1990s (Hughes, 1994; Steneck, 1994) – perhaps best marked by Bob Ginsburg's "Colloquium on coral reef hazards and health" (Ginsburg, 1993) – science, management, and conservation agencies became increasingly engaged in understanding the processes determining the fate of reefs. West and Salm (2003) raised the idea of resilience-based management (RBM), albeit without coining the term, and proposed that interventions should be directed toward reefs with less exposure to natural and anthropogenic disturbances and to focus interventions on the processes that confer resilience by either facilitating recovery or help resist stress and disturbance (McClanahan et al., 2012). RBM has now been defined as "using knowledge of current and future drivers influencing ecosystem function (e.g., coral disease outbreaks; changes in land-use, trade, or fishing practices) to prioritize, implement, and adapt management actions that sustain ecosystems and human well-being" (McLeod et al., 2019).

Research into coral reef resilience continues to blossom and appears to follow five trajectories. The largest is the quest to understand individual processes underlying reef resilience, both in isolation and as cumulative stressors. This literature is too large to be summarized here but includes research into connectivity, demographic rates, ecological interactions and stress responses (Andres and Rodenhouse, 1993; Roberts, 1997; Cowen et al., 2006; Nyström et al., 2008; Fabricius et al., 2011; McClanahan et al., 2011; Doropoulos et al., 2016; Ortiz et al., 2018). Second is the identification of empirical resilience metrics that can be used to compare reef sites (West and Salm, 2003; Obura and Grimsditch, 2009; Maynard et al., 2010; McClanahan et al., 2012; Jouffray et al., 2015; Guest et al., 2018). Third is the use of statistical models to predict community trajectories and infer drivers of resilience (Zychaluk et al., 2012; Cooper et al., 2015; Gross and Edmunds, 2015). Fourth is the development of mechanistic ecological models to understand and integrate the processes of resilience and/or predict reef trajectories under

multiple stresses (Mumby et al., 2007, 2014b; Anthony et al., 2011; Fung et al., 2011; Blackwood et al., 2012; Bozec and Mumby, 2015). Finally, a broader set of frameworks has become available to link resilience science to decision-making (Game et al., 2008; McLeod et al., 2009, 2012, 2019; Mumby et al., 2011; Anthony et al., 2015; Mumby and Anthony, 2015).

RESILIENCE CONCEPTS ON CORAL REEFS

There are three major usages of the term resilience in the coral reef and environmental literature. We introduce all three here in brief and then describe the behavior of the most popular in greater detail in a later section. The earliest usage of resilience considered the concepts of engineering and ecological resilience proposed by Holling (1996), which emerged from the modeling of predator-prey interactions revealing the ability of a system to undergo profound changes in community state (Holling, 1961, 1973; Lewontin, 1969; May, 1972). Engineering resilience refers to the time a system takes to return to a single equilibrium after a perturbation (Pimm, 1984; Holling, 1996). Ecological resilience considers the likelihood of the system (or social system, Marshall, 2010) to shift between multiple equilibria, separated by basins of attraction (**Figure 1**; Walker et al., 2002; Kinzig et al., 2006; Mumby et al., 2014b). A basin of attractor is a space in which the system tends to remain (Walker et al., 2004), see **Figure 2** for images illustrating coral-dominated and algal-dominated reefs. Ecosystems can move toward different attractors because of the numerous reinforcing feedbacks that drive their response even without external perturbations such as coral bleaching and storm damage.

The second usage of the word resilience is an umbrella term and considers the behavior of integrated socio-ecological systems, in which ecosystem dynamics might only be a single element amongst other components taken into consideration such as the role of human activity (Nyström et al., 2000; Folke, 2006). Resilience in this context has been described under the umbrellas of "resilience thinking" (Walker and Salt, 2006) or "panarchy" (Gunderson and Holling, 2001), and provides a framework to consider the factors that stabilize and drive a system. The key aspects of resilience thinking include resilience, adaptability (adaptive capacity) and transformability (Walker and Salt, 2006; Folke et al., 2010; Bellwood et al., 2012). The concept of panarchy refers to the hierarchical set of adaptive cycles at different scales and their effects across all scales (Gunderson and Holling, 2001). These frameworks do not explicitly invoke "ecological resilience," though multiple attractors may exist within the wider system or single components. Resilience thinking and panarchy provide a flexible framework to model complex systems and help identify metrics that confer resilience in social-ecological systems.

The third development of resilience on coral reefs is motivated by the ecological and social applications described earlier and seeks field-based metrics to ascertain the relative "resilience" of sites (Hughes et al., 2005; McClanahan et al., 2012; Jouffray et al., 2015; Maynard et al., 2015). Because such snapshot metrics do not quantify dynamical aspects of the system – which is the preserve of engineering and ecological resilience – they do not

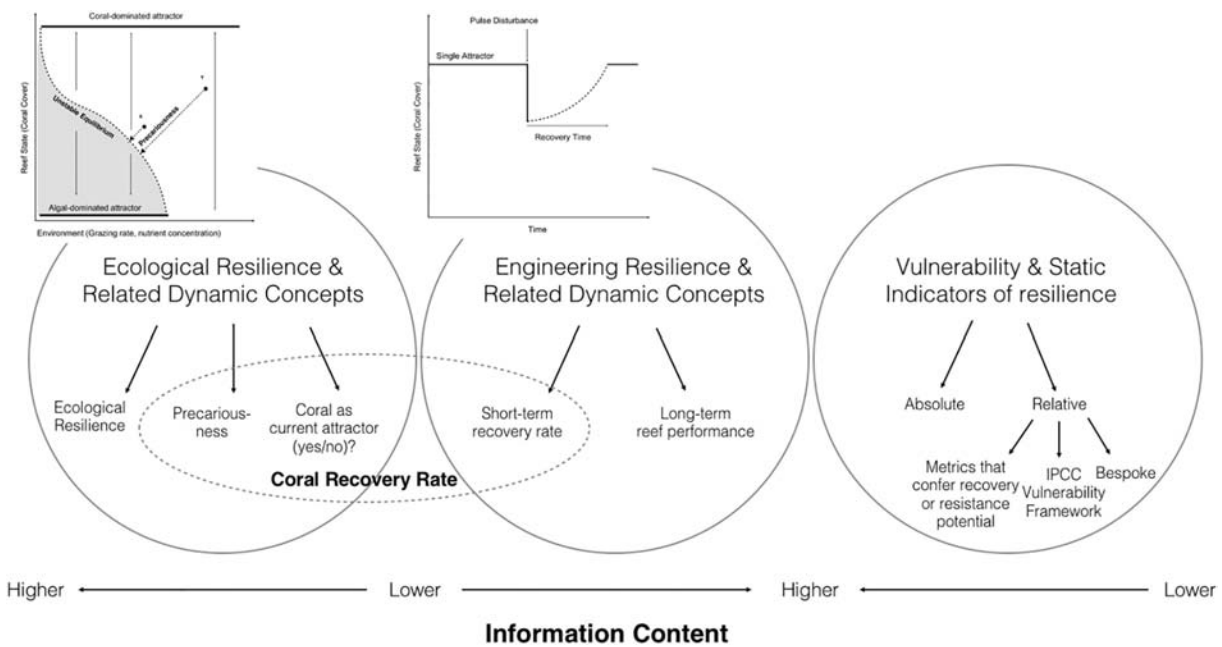


FIGURE 1 | Conceptual diagram of the various methods of measuring ecological resilience, engineering resilience and vulnerability. Precariousness is the distance of a reef to the suspected unstable equilibrium/tipping point. The precariousness of Reef X is greater than Reef Y. Reefs that fall in the shaded gray area has an algal-dominated current attractor, and reefs are in the white area has a coral-dominated current attractor. Dotted line represents cross-cutting methods that relate to coral recovery rate.

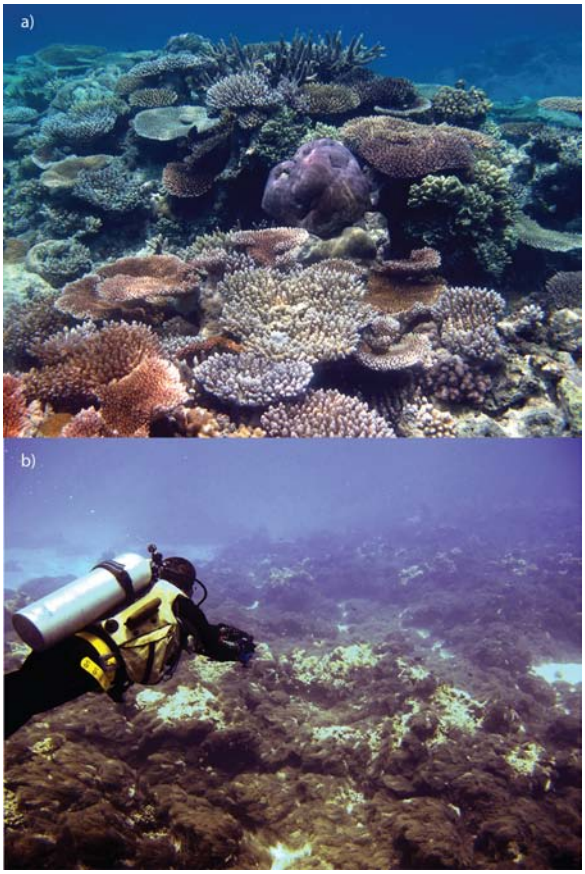


FIGURE 2 | Images showing **(a)** a coral-dominated reef and **(b)** an algal-dominated reef.

measure resilience directly; rather, they are useful in identifying sites that have a desirable set of metrics that indicate greater resilience. A major value of these descriptive approaches is that they do not depend on sophisticated models and are relatively easy to implement in the field. Since this approach does not quantify resilience *per se*, these approaches could be categorized as "vulnerability" measures (Mumby et al., 2014a). However, since the term resilience is so widely used for these approaches, we continue its use here adding the discriminators "recovery" and "resistance" metrics *sensu* McClanahan et al. (2012).

Vulnerability as an Alternative to the Resilience Concept

The concept of vulnerability emerged from the field of risk and hazard research (White, 1974), and is the "degree to which a system, subsystem, or system component is likely to experience harm due to exposure to a hazard, either a perturbation or stressor" (Turner et al., 2003). Because vulnerability is an encompassing concept warranting a number of measurement approaches (Alwang et al., 2001; Eakin and Luers, 2006), we discriminate between approaches that attempt to quantify the absolute vulnerability of a system versus those that create a relative measure of vulnerability. Obtaining an absolute vulnerability measure typically requires the specification of a critical threshold followed by an estimate of the probability of its transgression (Adger, 2006). Examples might be the probability that coral cover falls below 10% within the next decade, or the risk of flooding in coastal cities in 2050 (Hallegatte et al., 2013). Estimation of absolute vulnerability requires a system model, whether it be statistical, analytical or simulation-based. Moreover, the absolute vulnerability of a reef is context-dependent in relation to the coral community that dominates a reef (e.g., fast-growing and sensitive Acropora versus slow-growing and robust Porites), driven by a combination of biological and environmental drivers (e.g., Done, 1982; Gouezo et al., 2019). For example, using simulation modeling for coral communities on the Great Barrier Reef and the Caribbean, Ortiz et al. (2014) showed that the vulnerability of reefs to thermal disturbances was dependent on the diversity of coral functional groups.

The second approach to measuring vulnerability, which we term "relative vulnerability," often combines system metrics to compare vulnerability among sites or points in time. Here, the goal is not to calculate the absolute probability of an event occurring but rather to rank the relative vulnerability of sites and identify opportunities to reduce vulnerability (Eakin and Luers, 2006). A common way to measure relative vulnerability is to use the three components of the vulnerability framework: exposure, sensitivity and adaptive capacity (Adger, 2006; Cinner et al., 2012). Vulnerability is calculated using the equation "exposure + sensitivity – adaptive capacity," popularized by the Intergovernmental Panel on Climate Change (McCarthy, 2001). Exposure is the nature and degree to which a system is exposed to stressors; sensitivity is the degree to which the stressors affect a system (i.e., and is the opposite of resistance); and adaptive capacity is the ability of the system to adjust to the stressors or recover (Gallopín, 2006). Metrics are chosen to represent exposure, sensitivity and adaptive capacity, and are measured and combined to provide a relative index for comparison of sites (Cinner et al., 2012). Sensitivity and adaptive capacity may be estimated based on existing biological understanding of the systems in question. For example, Cinner et al. (2012) produced a sensitivity based on the proportion of households engaged in fisheries and whether households also engage in non-fisheries components. This method has been used to compare the vulnerability of fishing communities in face of climate change (Allison et al., 2009; Cinner et al., 2013) and to identify priority areas for management (Maynard et al., 2010, 2015). Alternatively, many studies also seek to estimate the relative vulnerability of sites with a bespoke framework using specific components selected to suit the purpose of the study (i.e., resilience metrics).

CONCEPTUAL FRAMEWORK FOR MEASURING REEF RESILIENCE AND VULNERABILITY

Following the major concepts of ecological resilience, engineering resilience, and vulnerability, a framework of reef resilience

quantification methods is proposed below and supported by case studies where applicable (**Figure 1**). Additional potential methods that have not been applied to reefs are also introduced under this framework. Note that we place empirical metrics relating to site resilience under "vulnerability" because they do not capture the dynamical properties of ecosystems but we agree that they can legitimately be described as resilience indices.

Ecological Resilience Related Approaches

Ecological Resilience

An emerging approach to calculate the resilience of coral reefs uses mechanistic ecological models to integrate available science. Mechanistic models can be used to ascertain whether multiple attractors are likely to exist and if so, predict the probability that a reef is pushed across tipping points within a specific period. This probabilistic approach embodies the original concept of ecological resilience (Holling, 1973) and is an alternative to quantifying the "level of disturbance" needed to tip a system, because the idea of measuring the "amount of disturbance" across multiple disparate forms of disturbance (bleaching, cyclones, etc.) is impenetrable (van Woesik, 2013). Rather, it is simpler to predict the probability of a system flipping attractor (see also van Nes and Scheffer (2007) who have developed a probabilistic approach to measuring the resilience of lacustrine (lake) ecosystems).

A number of models have been compared to independent time-series data for the Caribbean (Mumby et al., 2007; Kubicek and Borell, 2011) and Indo-Pacific (Melbourne-Thomas et al., 2011; Gurney et al., 2013; Sebastian and McClanahan, 2013; Ortiz et al., 2014). For instance, the ecological resilience of the Belize Barrier Reef was modeled and mapped under two levels of local management action (business-as-usual versus ban of herbivore fisheries) and two levels of action toward climate change (business-as-usual versus a green economy; Mumby et al., 2014b). Resilience was calculated as the probability that individual reefs would still be exhibiting coral recovery by 2030 (i.e., remaining under the attractor of a coral-dominated state even though coral dominance is never actually attained). The study found that implementation of a herbivore fisheries ban enacted in 2009 might increase the resilience of the reef sixfold, although the benefits were variable among reefs. The concept was further operationalized by identifying thresholds of herbivore harvest and size limits that maintain resilience in face of external disturbances (Bozec et al., 2016).

Precariousness

The prediction of resilience requires information on current system state, the location of underlying tipping points (unstable equilibrium, **Figure 1**), and predictive models of the disturbance regime. If the latter is unknown, an "instantaneous" measure of resilience can be obtained by estimating the distance of the reef to suspected tipping points. This is termed precariousness (**Figure 1**; Walker et al., 2004) and can be used as a relative measure of resilience among sites. The closer a reef sits from the unstable equilibrium, the more precarious it is. The measurement of precariousness requires a comparison of the current system state to known tipping points. Although precariousness has been suggested in the wider ecological literature (Walker et al., 2004; Hodgson et al., 2015), it has not been specifically measured for coral reefs. While the locations of unstable equilibria and thresholds have only been estimated for a very limited range of reefs, an interim approach might be to use the distance between a reef's current state and the "tipping points" identified for some Indian Ocean and Caribbean reefs for average system state against fish biomass (McClanahan et al., 2011; Karr et al., 2015). One advantage is that precariousness does not require the user to undertake modeling themselves. However, its shortcoming is the inability to account for exposure to external disturbances, such that two sites might lie equidistant from tipping points (i.e., same precariousness) with one having a greater risk of being perturbed and hence lower resilience. In summary, the technique has its merits as a simple tool to compare relative resilience of sites that share a similar disturbance regime (Yeung and Richardson, 2015).

Current Attractor

An even simpler approach than precariousness is to know whether the reef is likely to exhibit recovery or decline before the next disturbance. The current attractor identifies whether a reef is attracted toward the coral or alternative state at a point in time (**Figure 1**). If a snapshot of the reef state is available, then, like precariousness, the identification of the current attractor requires existing knowledge on the unstable equilibrium to identify which basin of attraction the reef currently sits in (i.e., coral-, algal- or sponge-attractors). In the absence of models of the ecosystem, it might be possible to estimate the existence of tipping points from statistical analyses of monitoring data; i.e., community states where reef trajectories are uncertain and variable showing either recovery or decline between disturbances (Zychaluk et al., 2012). Analyses of this type would require extensive data with at least short time series. The direction of each post-disturbance trajectory would allow the attractor to be identified at each initial state. Care must be taken not to confound this analyses with data from different physical environments where different attractors might occur (e.g., whereas a reef at 5 m might show recovery when coral cover is say 10%, a reef at 30 m might show decline when coral cover reaches an equivalent level). Moreover, a suite of early-warning algorithms have been developed to indicate whether a system is approaching a tipping point (Scheffer et al., 2009). The efficacy of such approaches, which often focus on critical slowing down of dynamics near tipping points, remain uncertain for coral reefs which are non-equilibrial ecosystems driven by massive episodic disturbance.

Engineering Resilience Related Approaches

The original definition of engineering resilience is impractical for coral reefs because reefs rarely attain a single coral-dominated equilibrium. However, two aspects of recovery rate can be operationalized. The first is a short-term recovery rate, usually measured directly from time-series. The second, termed reef performance, uses models to hindcast reef trajectories or

project into the future, typically over longer periods of time (Mumby and Anthony, 2015).

Short-Term Recovery Rates

Rates of change and trends have commonly been used to examine coral reef recovery and decline by tracking changes in coral cover over time (Emslie et al., 2008; Graham et al., 2011; Johns et al., 2014). Despite being easily applicable, simple averaging is problematic as calculated rates are highly influenced by the initial coral cover and assumes linear growth rates (Côté et al., 2006). A useful way to obtain short-term recovery rate is through statistical models that can incorporate ecological processes and dynamics such as multivariate autoregression models (Zychaluk et al., 2012; Cooper et al., 2015; Gross and Edmunds, 2015; Lam et al., 2018). Recovery is usually quantified using exponential rates to reduce the dependence on initial state, such as the instantaneous growth rate of a logistic growth function (Haddon, 2001). Reefs with faster recovery rates have higher engineering resilience. In a coral reef context, Mumby (2009) demonstrated that recovery rates increase the farther the system sits from a tipping point (though they can slow as they approach a stable equilibrium). Thus, recovery rates can also be used as an instantaneous proxy of ecological resilience irrespective of future disturbance, and are correlated to precariousness. It is important to distinguish the two approaches of short-term recovery rates and current attractor, although both relies on recovery rates, Current Attractor relies on impacts of disturbance and observations of the recovery trend immediately after the impact. Rates of short-term recovery are also related to the diversity of corals in any given system – dependent on the ocean geographical location being studied – as well as other ecological characteristics of the system such as fish diversity, system state following disturbance, and anthropogenic pollution (Bellwood et al., 2004; Fabricius, 2005; Graham et al., 2011, 2015). While short-term recovery rates cannot project reef state far into the future, they provide a useful basis for comparing the recoverability of reef locations (Ortiz et al., 2018). Moreover, while many studies rely on total coral cover as a single metric to examine return rate, it is also necessary to consider the type of community of corals in multivariate space or by functional groups (e.g., Ortiz et al., 2014; Tanner, 2017; Kayal et al., 2018; Gouezo et al., 2019).

Reef Performance

In many cases, including the GBR, the state of the reef might decline despite significant investments in reef management such as improvements in water quality (De'ath et al., 2012). Here, the value of management is best viewed using counterfactual analyses that ask how much worse the system would look had management action been reduced (Mumby et al., 2017). Or alternatively, how much healthier is the reef given our management interventions (**Figure 3**). Projecting how the reef might look into the future under different management scenarios provides a basis for management strategy evaluation. Mumby and Anthony (2015) proposed a framework that compares the trajectories of reefs under different levels of management and explicitly differentiates the degree to which local manageable stressors versus climate change and ocean acidification would contribute to loss of future reef state (see also Wolff et al., 2018). Such comparisons can also incorporate global differences in fish assemblages that result from different management strategies (Edwards et al., 2014; Harborne et al., 2018).

Because such methods are based on projections of reefs into the future they rely on models, even if simplistic. The goal is to compare alternative possible trajectories that might include (i) a purely natural system where the stressors could include cyclones but no climate change, (ii) the addition of climate change and ocean acidification, (iii) further addition of unmanageable local stressors (which may include historical accumulation of pollutants), and (iv) the further addition of potentially manageable stressors (e.g., anchor damage, fishing, crown-of-thorns starfish) (**Figure 4**). Reef performance simply expresses the average state of the reef under a one trajectory as a percentage of the reef's state under a less stressful trajectory. For example, a performance of 50% over the years 2020–2030 implies that coral cover under business-as-usual (all stressors) will, on average, be half of that in the absence of a pristine ecosystem between the years 2020 and 2030.

The approach can be applied irrespective of the existence of alternative attractors as it simply compares potential trajectories. Metrics of relative management potential can then be calculated and compared to inform decisions. This approach has been taken at a coarse scale on the Great Barrier Reef (Wolff et al., 2018), and is mostly limited by the spatial resolution of input data layers (particularly climate projections) and scientific understanding of the changes in reef state that management can elicit.

Vulnerability Related Approaches

Despite its roots in social science, the vulnerability concept is increasingly used in ecology (Beroya-Eitner, 2016) and thus incorporated in the proposed resilience framework (**Figure 1**). Vulnerability is context-specific (Barnett et al., 2008) and its measurement can be grouped into two general categories. Absolute vulnerability allows comparisons across space and time, whereas relative measures only indicate rankings and are

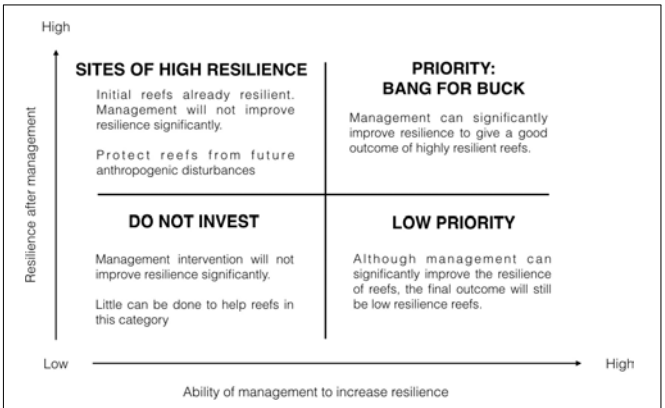
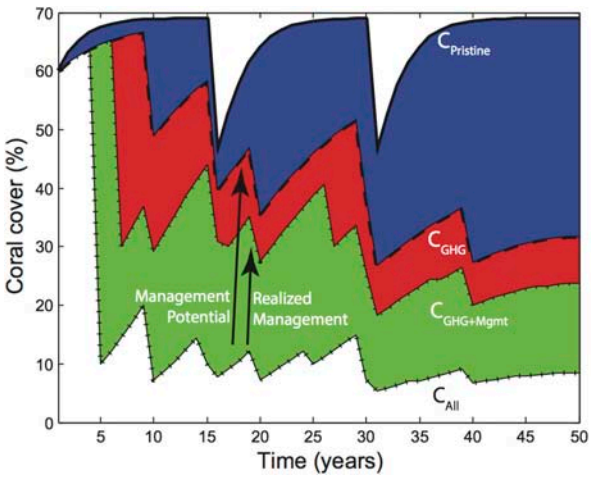


FIGURE 3 | Decision making framework for investment strategy for locations with varying resilience levels and potential management impact, modified from Mumby and Anthony (2015).



$$Ecosystem\ Performance_{ALL} = \frac{1}{T}\left[\sum_{t=1}^{T}\frac{C_{All}}{C_{Pristine}}\right].100$$

$$Ecosystem\ Performance_{GHG} = \frac{1}{T}\left[\sum_{t=1}^{T}\frac{C_{GHG}}{C_{Pristine}}\right].100$$

$$Ecosystem\ Performance_{MGMT} = \frac{1}{T}\left[\sum_{t=1}^{T}\frac{C_{GHG+Mgmt}}{C_{Pristine}}\right].100$$

$$Management\ Potential = Ecosystem\ Performance_{GHG} - Ecosystem\ Performance_{ALL}$$

$$Realized\ Management\ Impact = Ecosystem\ Performance_{MGMT} - Ecosystem\ Performance_{ALL}$$

FIGURE 4 | Use of Reef Performance metrics with modeled projections of reef futures with various levels of stressors (adapted from Mumby and Anthony, 2015). Results integrated over *T* time steps, *t*.

project/case-specific. It is useful to consider the suitability of using absolute or relative measures as data and skill requirements differ greatly (Alwang et al., 2001).

Absolute Vulnerability

A measure of absolute vulnerability can be achieved through simulation or statistical models, providing data are available for the appropriate parameterization. The measurement of absolute vulnerability requires an explicit benchmark (Alwang et al., 2001), such as the vulnerability of corals to an increase of 1°C in seawater temperatures, to physical hurricane impact, or any other specific kind of disturbance. This approach is best implemented using models, be they statistical or otherwise. System models are useful in quantifying vulnerability because the incorporation of explicit biological responses and ecological interactions lend themselves to projecting the response of a system into new environments (Scheffer and Carpenter, 2003; Nyström et al., 2008). One example of an absolute vulnerability measurement in coral reef ecosystems is estimation of the number of years before coral cover fell below 10% in Belize (Mumby et al., 2014b). Statistical approaches offer an alternative to simulation models for understanding system dynamics. For example, Zychaluk et al. (2012) used a Markov process to project the average trajectory of coral reefs toward coral, algal or other endpoints. Alternative model formulations are also being used to incorporate a greater range of covariates (Cooper et al., 2015), explore reef ecosystem stability in response to multiple disturbances (Gross and Edmunds, 2015), and to determine trajectories using Bayesian methods through reef accretion and recovery following disturbance (van Woesik, 2013).

Relative Vulnerability and Resilience Indices

Most published assessments of reef resilience utilized relative vulnerability and identified a series of reef attributes that confer resilience. Attributes are measured in the field, scored and aggregated to provide an overall "resilience metric" at each reef location. Attributes are chosen by literature review (Obura and Grimsditch, 2009), collegial expert opinion (McClanahan et al., 2012), consultation of fishermen to anticipate social-economical responses to change (Marshall and Marshall, 2007), and relevance to geographic location (Maynard et al., 2010). As vulnerability approaches stems from social science, studies under this category most readily incorporate both human stressors in addition to environmental and ecological factors. Individual attributes are often weighted by importance prior to integration (Maynard et al., 2010; McClanahan et al., 2012). For example, Maynard et al. (2010) created an empirical framework where resilience attributes (indicators) were classified, ranked and weighted following scientific evidence. The final resilience score is simply the sum of all weighted scores. The great benefit of this metrics approach (i.e., relative vulnerability) is that it can be measured easily in the field and used to rank the vulnerability of sites (Beroya-Eitner, 2016). Like all the approaches reviewed, it has some limitations and caveats (**Table 1**), which are well known by implementers of these methods.

Most resilience indices do not measure ecological processes directly; rather they focus on state (e.g., coral cover) or proxies of process (e.g., fish biomass for herbivory). Not surprisingly, it is preferable to use the closest proxy to the process as possible. For example, a study of the association between herbivory and juvenile coral density on Caribbean reefs found that better metrics explained were three times more successful at resolving the relationship (Steneck et al., 2018). Parrotfish biomass only explained 8% of the variance of juvenile coral density whereas a metric that accounted for parrotfish species and size effects on grazing, and the surface area of grazable substrate explained 23% of variance.

Although the use of weightings can emphasize the disproportionate importance of some processes over others (Maynard et al., 2010), an implicit assumption remains that processes integrate linearly (Barnett et al., 2008). In reality,

reinforcing feedback mechanisms are important drivers of coral reef dynamics (Mumby and Steneck, 2008) and tend to generate non-linear interactions among processes (Birkeland, 2004). For example, the outcome of having a "high" value for coral larval supply depends strongly on the processes that influence settlement and post-settlement mortality, such as macroalgal cover (Dixon et al., 2015; Doropoulos et al., 2015) and corallivory (Doropoulos et al., 2016). The non-linear and context-dependencies among processes are more easily dealt with using mechanistic models. It is also important to recognize that vulnerability assessments are sensitive to the number of metrics included; the more metrics included, the less any particular attribute can influence the overall score (McClanahan et al., 2012). Yet an extreme value for one attribute (e.g., macroalgal cover) might be sufficient to reduce recovery severely (Mumby et al., 2015).

Metrics are often assumed to be uni-directional, but factors can affect resilience in both directions depending on context and environment (**Table 2**). For example, ocean currents that contribute to connectivity may also become a threat to resilience by carrying pollutants, nutrients and diseases (Nyström et al., 2000; McClanahan et al., 2002). Finally, while the empirical nature of vulnerability metrics approach is appealing, its dependence on field surveys tends to make it difficult to scale up. This is the converse problem with modeling studies which have large spatial extent but limited resolution at small-scales. Ultimately, the choice of approach (or approaches) will be determined, in part, by the scale or scales at which management is focused. Recent studies have advocated a nested approach that makes this explicit (Maynard et al., 2015).

APPLICATION OF RESILIENCE ASSESSMENTS TO REEF MANAGEMENT

The multiplicity of methods for resilience assessments has outpaced their incorporation into management. Each resilience method can be used to answer a suite of management questions (**Table 3**). Commonly, the end-point for many resilience assessments is a map of ranked vulnerabilities or "resilience metrics," yet the pathway for these metrics to be incorporated into management decisions can be unclear. There has been some consideration on how to prioritize depending on the level of threats expected. Game et al. (2008) and Anthony et al. (2015) put forward comprehensive frameworks for the management process. What appears to be under-developed is formalizing the

TABLE 1 | Implicit underlying assumptions of the relative vulnerability approach.

	Metric approach analysis	Implicit assumptions/potential issues	References
Choosing attributes	1. Literature review	Ecosystem drivers in literature were from comparable system (physical environment, biodiversity, etc.) to that being evaluated. Good to discriminate whether factor influences recovery or resistance.	Obura and Grimsditch, 2009; Maynard et al., 2010
	2. Expert opinion ranking	Experts correct and that collective opinion is consistent and not a compromise such that attributes might not align with any individual opinion	Marshall and Marshall, 2007; McClanahan et al., 2012
	3. Other management consideration of ecological services, e.g., carbon sequestration	Will vary amongst approaches depending on the focus of programmes	Programmes within organizations
Combining attributes	1. Combining values of different attributes to get an overall resilience score	Linear relationships between attributes; score is a direct measure of resilience	
	(a) Without weighting	All attributes contribute equally to resilience	Obura and Grimsditch, 2009
	(b) With weighting	Weightings appropriate and attributes interact linearly	
	(i) Ecological importance from literature	Ecosystem drivers in literature were from comparable system (physical environment, biodiversity, etc.) to that being evaluated; relative importance of attributes appropriate	Maynard et al., 2010
	(ii) Scientific evidence from literature/expert opinion	More studies on one attribute might elevate its perceived importance	McClanahan et al., 2012; Cinner et al., 2013
	2. Overall resilience scores classified into resilience categories (low, mid, high) based on predetermined ranges of overall scores	Linear relationships; overall scores directly translate to resilience categories	Maynard et al., 2010; Mamauag et al., 2013
	3. Comparison of individual attribute scores with no overall resilience score provided	No indication of the importance of each attribute to resilience	Bruckner, 2012
Link to management	1. Identified reef sites with the lowest to highest resilience	Score is a direct measure of resilience; does not link to further management actions.	Obura and Grimsditch, 2009; Obura and Grimsditch, 2009; McClanahan et al., 2012
	2. Ranked "management influence potential" to determine how management can influence the resilience of a reef site	The potential to be managed ranking directly influences the resilience of the systems	Maynard et al., 2010

TABLE 2 | Variables used in resilience assessments that can have both positive and negative effects on resilience.

Variable	Reasons for affecting resilience			
	(+)	References	(−)	References
Corals exposed at low tide	Promotes acclimatization and resistance	West and Salm, 2003; Obura and Grimsditch, 2009	Corals exposed to air for long periods causes mortality	Maynard et al., 2010
Currents	Coral larval transport;	West and Salm, 2003; Obura and Grimsditch, 2009	Transport pests like crown-of-thorns starfish	Hock et al., 2017
	Temperature regulation	Obura and Grimsditch, 2009	Carry pollutants, nutrients and diseases	Nyström et al., 2000
	Prevent excessive buildup of toxins from bleaching	West and Salm, 2003		
Mature colonies	Mechanically stronger	McClanahan et al., 2011	More susceptible to bleaching	Mumby, 1999; McClanahan et al., 2011
	More recruits produced	Maynard et al., 2010		
	Likely to have withstood a number a range of stressors and hence more resistant	Maynard et al., 2010		
Sea urchins	Herbivory	Obura and Grimsditch, 2009; Maynard et al., 2010; McClanahan et al., 2012; Graham et al., 2015	Bioerosion	West and Salm, 2003; Obura and Grimsditch, 2009
Turbidity/ Sedimentation	Less light penetration, less exposure to thermal stress	West and Salm, 2003; Obura and Grimsditch, 2009	Corals require physiological resources to tolerate sediments, which would increase its susceptibility to other stressors	Maynard et al., 2010
			Limits coral settlement	Birrell et al., 2005; McClanahan et al., 2012
Upwelling	Reduces thermal stress during bleaching	Maynard et al., 2010; McClanahan et al., 2012	Corals in upwelling areas more sensitive to temperature increases	West and Salm, 2003
	Cooling	West and Salm, 2003		
Wave exposure/energy	Increase oxygenation in water, enhances coral metabolism	Obura and Grimsditch, 2009	Promotes algal growth	Mumby et al., 2014b; Graham et al., 2015
	Promotes water movement to flush toxins	West and Salm, 2003		
	Algal dislodgement	Graham et al., 2015		

+ and − indicates a positive and negative effect on resilience respectively.

link between the nature of a management intervention and its expected influence on resilience (or vulnerability).

A useful attempt to operationalize RBM utilized a metrics-based approach and identified metrics that were under potential management control and scored the likely ease of implementing such management at the site (Maynard et al., 2010). Another key consideration would be the degree to which management would improve the outlook or resilience score if implemented. Mumby et al. (2014b) specifically simulated the impact of a change in fisheries policy and mapped the expected increase in resilience across the reef. Mumby and Anthony (2015) went further and suggested management prioritizations would benefit from a simple framework that plotted current state or resilience on one axis and the degree to which management could improve that state or resilience on the other (**Figure 3**). A given management intervention would achieve the greatest "bang for buck" where the scope for increasing resilience is maximized. Similarly, areas of low resilience that cannot be improved by management would receive a low priority for intervention.

A similar strategy to estimate the benefits of management implementation could be developed for metrics-based approaches. In addition to a site's current vulnerability score, it would be possible to estimate the degree to which an intervention might increase that score, subject to local constraints. For example, a site might only have a standardized herbivory score of 0.5, implying intermediate herbivorous fish biomass. Were a marine reserve to be established, herbivory would be expected to increase to the maximum score possible subject to limitations of the benthos, such as the local habitat complexity and the availability of food (cover of algal turfs). The researcher might turn to relevant analyses of bivariate relationships between variables to estimate these constraints; i.e., the relationships between herbivore biomass, habitat complexity, and algal cover (McClanahan et al., 2011; Karr et al., 2015). The outcome might be that herbivory could increase to a value of 0.8, which when combined with other influences of a reserve on other metrics, leads to a new vulnerability measure, "potential vulnerability if management enacted." Moreover,

TABLE 3 | Management questions that can be answered using different resilience frameworks.

Management questions	Ecological resilience	Precarious-ness	Current attractor	Short-term recovery rate	Reef performance	Absolute vulnerability	Relative vulnerability/ resilience indices
Will coral cover continue to increase given no disturbances?	✓	✓	✓	✓	✓	✓	×
What is the resilience of the reef at a future point in time?	✓	×	×	×	✓	×	×
What is the likely state of the reef in the next 2–3 years?	✓	✓	✓	✓	✓	✓	×
What is the likely state of the reef in the next 10 + years?	✓	×	×	×	✓	✓	×
How much greater is the resilience of reef X versus reef Y?	✓	×	×	×	✓	×	×
Which reefs *are likely* to have the greatest resilience?	✓	×	×	×	✓	×	✓
Where might no-take reserves have the greatest benefit on reef resilience?	✓	✓	✓	×	✓	✓	✓*
To what extent will improvements in water quality (or another management intervention) improve reef resilience?	✓	×	×	×	✓	✓	×
Which management intervention would improve reef resilience the most?	✓	×	×	×	✓	✓	✓*,**

*Note that "precariousness" and "current attractor" have not yet been implemented on coral reefs. *Requires a modified approach to simulate how the change in management will alter the final scores for relative vulnerability. **Sensitive to how the integration of different attributes accurately represents the response of the reef ecosystem.*

alternate attractors are not always between coral and macroalgal dominated states. For example, transitions from coral to other organism assemblages have been documented throughout the globe and include shifts to corallimorphs, soft corals, sponges, urchin barrens, sea anemones, and ascidians (Norström et al., 2009). Management interventions to reduce the probability of these transitions remaining stable require different strategies to managing transitions from corals to macroalgae.

To move toward strategic management planning, predictive approaches that link interventions to probable future reef responses would be useful. Given that the use of empirical metrics is the most widely-used resilience quantification approach, scientists need to facilitate the efficacy and predictability of metrics-based approaches. We believe there has not yet been a study to resolve which metrics has the most predictive power, and a meta-analysis is long overdue. As the key metrics are resolved, studies can take into account the relative influence of metrics on resilience and produce a more nuanced analysis based on the interactions of multiple metrics. There are specific examples finding rugosity and herbivory to be predictors of flipping to from coral-dominated to algal-dominated attractors. Studies from the Caribbean and Pacific have both found algal turf canopy height to be a good predictor of coral recruitment failure, as well as macroalgal cover. Most resilience indicators are snapshot datasets, such as biomass, cover, and structural complexity. In some cases it is hoped that data like herbivore biomass is a reasonable proxy of herbivory (though see Steneck et al., 2018, for its limitations). Yet longer-term data on key processes, such as calcification – derived from coral cores – have rarely (if ever) been used as part of a resilience/vulnerability assessment. It would be instructive to evaluate the predictive power of such metrics as good indicators of, say exposure to stressful environments. One challenge is to create a more sophisticated but accessible method for the integration of attribute values that captures the complex non-linear interactions of physical, biological and ecological processes on reefs (Barbier et al., 2008; Nyström et al., 2008). This could be achieved by coupling ecological models with an interface that allows users to enter their attribute data and receive a prediction of resilience or recovery rate. Some attempts have been made to provide a means of diagnosing and interpreting reef ecological data, but these remain in their infancy (Flower et al., 2017). A more formal quantitative approach would utilize monitoring datasets from specific reefs into a larger statistical framework – such as Bayesian Belief Networks (Wooldridge and Done, 2004; Renken and Mumby, 2009) – capable of making short-term predictions for a given reef's outlook based on local environmental effects, current state, and disturbance history (Eason et al., 2016). Such statistical models would not only help practitioners identify appropriate resilience attributes for a given context, but they would help utilize the vast amounts of monitoring data available. And importantly, by providing a tool to help understand reef resilience, they would provide an incentive for practitioners and scientists to contribute their data and build a community-wide understanding of the drivers of reef health in different environments.

AUTHOR CONTRIBUTIONS

PM and VL conceived the original idea. VL conducted the literature review, collected the data, and wrote the manuscript. PM discussed and provided inputs on the interpretation of the results and co-authored the manuscript. CD and Y-MB discussed ideas and edited the manuscript.

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Evaluating Resilience Co-benefits of Engineering With Nature® Projects

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An increasing abundance of projects demonstrate that coastal management strategies that align engineering and ecological objectives can deliver a wide range benefits. Better understanding how these strategies fare under stress is crucially important, including in comparison to more conventional coastal engineering approaches, in order to inform where they might be a viable alternative or complement to conventional coastal storm risk management. In particular, the prospect that these strategies may be able to recover from disturbances and adapt to better survive future disturbances with minimal or no intervention is compelling. However, no formal accounting method exists to assess how ecosystem-based approaches contribute to the resilience of coastal systems, that is, their ability to prepare, absorb, recover, and adapt from stressors. An assessment rubric is developed and demonstrated for Engineering With Nature® projects and limitations and ways forward are discussed.

Keywords: resilience, co-benefits, coastal management, natural infrastructure, risk

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INTRODUCTION

The co-existence and also clash of human activity and ecosystems at the interface of the land and ocean raise questions about how best to achieve balance among multiple coastal management objectives while maximizing benefits. Thinking about how to preserve human activity (e.g., shipping, tourism, energy exploration, fisheries, and others) in spite of hazards associated with coastal zones (i.e., energetic storms and inundation by rising sea levels) while reducing conflict with ecosystems is evolving. This is in part because highly engineered systems that interface with natural forces have sometimes proven brittle and while stronger, more robust solutions exist, they may come with exorbitant costs and may only delay brittle failure. At a time when coastal infrastructure is in need of investment and updating, decision makers have the opportunity to invest in natural and nature-based infrastructure to increase resilience and provide cost-effective critical services (Sutton-Grier et al., 2018). Efforts to better align the delivery of engineering objectives with environmental and social objectives abound in the United States, Europe, and are burgeoning worldwide (Bridges et al., 2018). They are demonstrating that strategies to enhance ecosystems and leverage natural processes can deliver a wide array of environmental, social, and economic benefits in a cost-effective manner. However, there is an enduring research need to examine how they perform under stress; for example, determining how natural and nature-based systems perform with respect to resilience goals has not been sufficiently explored. This paper examines the challenge of quantifying resilience benefits of coastal projects, develops an assessment method suited to existing projects, and discusses ways forward to meet the challenge.

USACE and the Nation's Coastlines

These questions are salient to the United States Army Corps of Engineers (USACE), which plays an important role in coastal management in the United States, as the coastal zone is where its missions are often applicable and overlapping. The USACE is responsible for conducting and operating civil works projects to maintain the navigability of the nation's waterways to support economic activity, reduce riverine and coastal flooding risk to minimize property damage and loss, and restore and manage aquatic ecosystems. The work to achieve these missions exists in tandem with complex natural and human dynamics including sediment processes, natural hazard risk prediction, and cost benefit trade-offs, among others complicating factors.

The USACE and other organizations are exploring new approaches to achieving agency missions in response to these present-day realities, a trend that is in line with the evolving policy and practice of incorporating nature-based approaches in Europe as well (Nesshöver et al., 2017). Engineering With Nature® (EWN®) is an initiative of the USACE that aims to investigate, demonstrate, and support the design of projects that meet engineering and mission objectives but also seeks to provide environmental benefits and enhance long-term sustainability. EWN efforts take a variety of forms to support water infrastructure projects, but share that they pursue "intentional alignment of natural and engineering processes to efficiently and sustainably deliver economic, environmental, and social benefits through collaboration" (Bridges et al., 2018). The overarching strategy is to use natural processes to achieve engineering objectives or to use human design to emulate natural features and functions, better aligning projects with nature and yielding greater value by addressing multiple objectives.

An important motivation for the EWN initiative is to more fully account for the array of environmental, economic, and social benefits that are generated by USACE projects (Foran et al., 2018), and to promote designs that can achieve numerous co-benefits. The initiative does so by enumerating benefits that may not be fully accounted for in common applications of 1983 Economic and Environmental Principles and Guidelines for Water and Related Land Implementation Studies and made generally on the basis of economic valuation (Narayan et al., 2017). The range of benefits of EWN projects include flood risk reduction, recreation, wildlife habitat, fish habitat, reduced shoreline erosion, navigation safety, plant habitat, and aesthetic value, among others (Bridges et al., 2014).

A co-benefit of increasing interest to the USACE and other organizations is resilience[1], which can be derived from EWN projects (Bridges and Chasten, 2016). Resilience benefit to communities is expected to emerge from the enhancement of coastal ecosystems, the intention of which is both anthropocentric and eco-centric. The two categories are not mutually exclusive (Sutton-Grier et al., 2015), as has been articulated by the concept of "ecosystem goods and services" – that humans benefit directly or indirectly from the existence and functioning of ecosystems (Fisher et al., 2009). There is a vast body of literature that seeks to define and enumerate the benefits that humans derive from functioning ecosystems, especially so that they can enter systems of formal accounting that accompany assignment of economic valuation to projects (see literature review by Tazik et al., 2013). While the philosophy of EWN intuitively intersects with the concept of resilience, a formal approach does not exist for aligning resilience outcomes with EWN projects, as difficulty arises from how resilience should be applied via ecosystems for different types of hazards, which occur on different time scales, threaten systems with different stress thresholds, and have institutionally entrenched methods for managing them.

Conventional and Nature-Based Approaches to Coastal Risk Management

For coastal communities, flood hazard stems from the occurrence of storm surge and heavy precipitation that accompany coastal storms and loss of land mass to subsidence, coastal erosion, and sea level rise (Neumann et al., 2014). Coastal engineering is intended to provide defense against coastal flood risk and is designed to protect built infrastructure and human life from exposure to the full extent of coastal hazards (floodwaters, wind, etc.). The necessity of coastal defense is evident. In 2010, 39% of the 313 million people in the United States lived in coastal counties and 52% lived in coastal watershed counties; additionally, economies in coastal communities account for approximately $8.3 trillion in goods and services (National Oceanic and Atmospheric Administration [NOAA], 2019). However, an approach that relies predominantly on conventional structural measures to exclude floodwater and dissipate wave energy (e.g., with seawalls and breakwaters) is being called into question for several reasons. Among them are that achieving desired levels of protection is increasingly costly and that coastal structures can interfere with natural dynamics that maintain coastlines and land elevation (Temmerman et al., 2013) and can impact coastal ecosystems (Gittman et al., 2016).

Ecosystem-based coastal protection measures may be a viable alternative or complement to conventional coastal storm risk management and are being explored as such. Effective risk management reduces the parameters of risk, which is conceptualized as the product of hazard, vulnerability, and consequence (Willows et al., 2003). In their cost-benefit analysis of defense measures, Reguero et al. (2018) defines risk mitigation benefit in the context of coastal disasters as being derived from (1) hazard reduction via wave and surge attenuation, (2) physical protection from floods; and/or (3) physical exposure aversion. In their review, Shepard et al. (2011) found salt marsh protections that correspond with Reguero et al. (2018) risk mitigation benefits: wave attenuation as measured by reductions in wave height, and shoreline stabilization as measured by accretion, lateral erosion reduction, and marsh surface elevation change. Shepard et al. (2011) concludes that coastal ecosystems should

[1]The culmination of many events motivates USACE's work to enhance resilience: lessons learned from devastating hurricanes such as Katrina and Sandy, Department of Defense (DoD) and executive branch policies emphasizing continuity of critical infrastructure functions, and greater recognition that uncertainty, complexity, and changing conditions complicate our ability to meet various objectives. The 2016 Resilience Initiative Roadmap establishes that resilience thinking should be implemented USACE-wide and work to mainstream the concept into USACE operations is ongoing.

be mobilized and protected by policy makers for economic and societal benefits. Further, studies that employ modeling aim to translate wave and storm surge attenuation to into efficacy and expected reduction in damages (Barbier and Enchelmeyer, 2014; Barbier, 2015; Vuik et al., 2016; Narayan et al., 2017; Reguero et al., 2018). Pontee et al. (2016) provides a small survey of diverse nature-based projects and reports lessons learned while Saleh and Weinstein (2016) review the literature on tidal wetlands, thin-layer placement, and living shorelines and also reports mixed results from a coastal protection perspective. Few studies, however, have compared the actual performance of ecosystem-based coastal protection to conventional measures. Gittman et al. (2014) compared the performance of North Carolina shoreline protection measures during Hurricane Irene (a category 1 hurricane) and found that marshes with and without sills suffered less erosion than bulkheads. More direct studies are needed to build the evidence base of where and under what circumstances ecosystem-based approaches can outperform or supplement their conventional counterparts.

Despite increasing efforts to mitigate the impact of natural disasters, losses suffered continues to rise (National Oceanic and Atmospheric Administration [NOAA], 2018). In fact, this reality is the primary motivation for United States and worldwide policies that set resilience management objectives (Bakkensen et al., 2017; Linkov and Trump, 2019); the inadequacy of risk management alone to reduce losses points to the need for new objectives related to maintaining system functions to their greatest extent in spite of disruptive events. In 2013, the USACE Chief of Engineers charged the Coastal Engineering Research Board (CERB) to strategize integrating risk reduction and resilience into Corps practices (Rosati et al., 2015). In their definition of resilience, the National Academy of Sciences (NAS) (National Research Council [NRC], 2012) stress the abilities to prepare and plan for, absorb, recover from, and more successfully adapt to adverse events. These cycles correlate with the definition of resilience considered by the CERB (Rosati et al., 2015) and capture the temporal dimension of resilience (Linkov et al., 2013). Action and infrastructure generally assigned to flood risk mitigation contribute to preparation for weather events and reduction of damages but do not extend to recovery and adaptation. Therefore, efforts to meet resilience objectives seek measures that improve systems along the entire lifecycle of a disaster. An assertion about the potential of ecosystem-based coastal defense to contribute to resilience has emerged and warrants further investigation, particularly given that it is already being considered as an alternative to conventional engineering solutions for the reasons described above (Spalding et al., 2014).

Defining Resilience for the Purpose of Measurement

Answering the question of how coastal ecosystems and ecosystem-based approaches to coastal management contribute to the resilience of a system requires teasing out and delineating the "system" and what it should be resilient to. In other words, the "resilience of what, to what" as was posited by Carpenter et al. (2001) almost two decades ago. Resilience broadly concerns how systems respond to stress, both acute and chronic. While many fields have expressed that the concept may be useful for describing and managing systems (communities, infrastructure, psychology, ecosystems, etc.), its adoption as a management objection has raised various debatable points: what constitutes a resilient outcome; can the resilience of a system to stress be predicted; are there attributes or indicators of a resilient system; what conditions or actions will foster resilient outcomes; and others.

A large and growing body of literature works through these questions (e.g., see Walker and Cooper, 2011; Liao, 2012; Kress et al., 2016; Timpane-Padgham et al., 2017) and includes efforts to describe similarities, differences and interactions between the resilience of engineered and ecological systems (Holling, 1996; Angeler et al., 2018). Key differences stem from the nature of the objectives of the respective disciplines - the study and practice of engineering is prescriptive and assumes that resilience is normative whereas ecology is descriptive and more agnostic about stability. Hence, engineered systems are deliberately managed to achieve and maintain a single stable state and are generally recovered back to their original state following damage whereas ecological systems are observed to be capable of multiple states of variable stability (Pendall et al., 2010; Meerow et al., 2016). The two types of systems are not necessarily discrete, as has been recognized by resilience typologies such as socio-ecological resilience (Davidson et al., 2016).

The goal of our current research effort is to develop and demonstrate a rubric that is generally applicable to EWN projects and other ecosystem-based coastal features that vary greatly in their form and function. In terms of formulating an assessment method for EWN projects, bounding the problem serves to reduce some of the indeterminacy of the concept of resilience benefits of coastal ecosystems. Resilience is considered primarily with respect to the well-being of proximal communities in the presence of coastal hazards. More specifically, resilience is expected to emerge from:

- Buffering the built environment from/reducing the impact of coastal stressors and shocks by absorbing energy;
- Persistence of coastal features (including by robustness to impact, recovery and adaptation), mainly via sediment processes (stabilizing and/or accreting sediment); and
- Adaptability of landforms by natural or human means.

By using the resilience considerations mentioned above, a rubric was developed and applied to EWN projects as an attempt to better understand the performance of EWN projects in terms of their contributions to coastal ecosystem management.

CASE STUDY RESILIENCE EVALUATION

Methodology

Since 2010, over 250 civil engineering projects in both coastal and inland environments in the United States and worldwide have employed practices consistent with EWN principles. Project details are documented and accessible via the EWN Project Mapper (ProMap), an online database and map

viewer developed by the USACE, including site descriptions, associated infrastructure project types, engineering features, project benefits, and links to supplemental resources[2]. Project information in ProMap is sourced from a variety of resources, and thus content quality and quantity varies considerably among projects. For this reason, not all project descriptions contained the data and other information necessary to perform the evaluation; information was adequately detailed for 89 coastal projects, the majority of which are marine. Each was reviewed to determine the specific engineering strategies that were implemented. The engineering strategies were then summarized as a list of 27 feature types (**Figure 1**). Feature types are generally defined by feature's coastal engineering form (e.g., breakwater, levee, and groin) and the specific aspect that indicates that the engineering involves nature (e.g., incorporates habitat opportunities, beneficially re-uses dredged sediment, relies on the functioning of natural elements to achieve engineering objectives). Each project was assigned at least one feature type (note that the number of projects that are grouped into feature type is in parentheses next to feature type labels in **Figure 1**). For example, the Vermillion Bay Oyster Reef Restoration project in New Orleans, LA, United States utilized reef modules to restore oyster reefs and provide a habitat for fish. This engineering feature type was categorized as "breakwater constructed with modified concrete blocks that allow habitat growth opportunities". Feature types were formulated to group similar projects while retaining a sufficient level of detail to be informative about how project designs intend to achieve multiple and synergistic objectives.

Each engineering feature type was evaluated for its contribution to (1) resilience and (2) USACE business lines (i.e., flood risk management, navigation, ecosystem restoration). A rubric was developed for assessing the resilience contribution of EWN feature types. It disaggregates resilience into four phases of the disaster lifecycle as defined by the NAS (National Research Council [NRC], 2012) – plan/prepare, absorb, recover, and adapt – and suggested as appropriate for capturing the temporal dimension of resilience (Linkov et al., 2013). Indicators of resilience were developed to capture the expected ability of feature types to prepare for and absorb shocks, recover from damages, and adapt to better prepare for future conditions and shocks. Indicators were derived from a report of the Environmental Defense Fund (EDF) that used literature support and expert judgment to evaluate the strengths, known weaknesses, uncertainties, and suitable conditions of engineered coastal features as methods for risk reduction (Cunniff and Schwartz, 2015). That report summarizes the outcomes of a workshop of 19 subject matter experts including scientists, engineers, program managers, and financiers that provided insight into the performance of natural infrastructure and nature-based features and supplemented with a review of literature on the same subject. In order to create an assessment rubric, all of the beneficial qualities of coastal features were assigned to a NAS resilience category. Descriptions in the EDF report generally contained terms that could be aligned to a temporal scale of disturbances. Similar benefits were summarized into indicator statements so they could be applied to the EWN projects (**Table 1**). The coastal features evaluated in Cunniff and Schwartz (2015) and the feature types used in this research are generally similar and therefore the beneficial qualities (i.e., indicators) were assumed to be extendable to EWN project evaluation. A tally was generated for feature type to quantify how many indicators of resilience each was judged to possess. As an example, the Hart-Miller Island, which is located near the mouths of Back and Middle rivers near Baltimore, MA, United States, was developed with placement of dredged material. The island was categorized as a "barrier island" and barrier islands have characteristics that align with all of the indicators of absorbing stress and shocks: dissipate wave energy from coastal storm surges, protects the shoreline from erosion, and acts as a wind break for the adjacent community. Project-level information contributed to the appropriate designation of feature type(s) and feature types were assessed in aggregate. Some of the weaknesses identified in the EDF report are included in the discussion section of this paper.

An additional set of indicators was developed to account for the contributions of EWN projects to select USACE civil works programs (**Table 2**), which are essentially civil works objectives, with the goal of gaining insight into which types of USACE projects might have the most resilience contribution. Three business lines were chosen for the assessment: navigation management, environmental restoration, and a combination of flood management and coastal storm risk reduction, the latter two being distinguishable programs that have overlapping missions and benefits. The indicators of which business line(s) a project services were developed based on literature from the USACE including a technical report on the use of natural-based features to support coastal resilience (Bridges et al., 2015).

Each of the 27 EWN features types was assessed along the 12 resilience indicators and 10 USACE business line indicators. Feature types receive a binary 0–1 score for each indicator, where 1 was assigned primarily on whether the EDF report attributed a particular kind of benefit to a feature. Scores were summed for resilience and business line, respectively, such that total scores are the number of indicators each feature type was found to have. Each EWN project received the same score as their respective feature types. Some EWN projects implemented more than one of the 27 engineering features listed in **Figure 1** and therefore received points for meeting the same indicator more than once. In these instances, the score received for that specific indicator was normalized to 1.

RESULTS

Results of the resilience assessment of EWN features indicates that they tended to score higher in the planning/prepare, absorb, and adapt aspects of resilience and lower in their ability to recover. As indicated in **Figure 1**, only 3 of 27 feature types had any indicator of recoverability: dune restoration/reconstruction

[2]Link to EWN ProMap: https://ewn.el.erdc.dren.mil/ProMap/index.html.

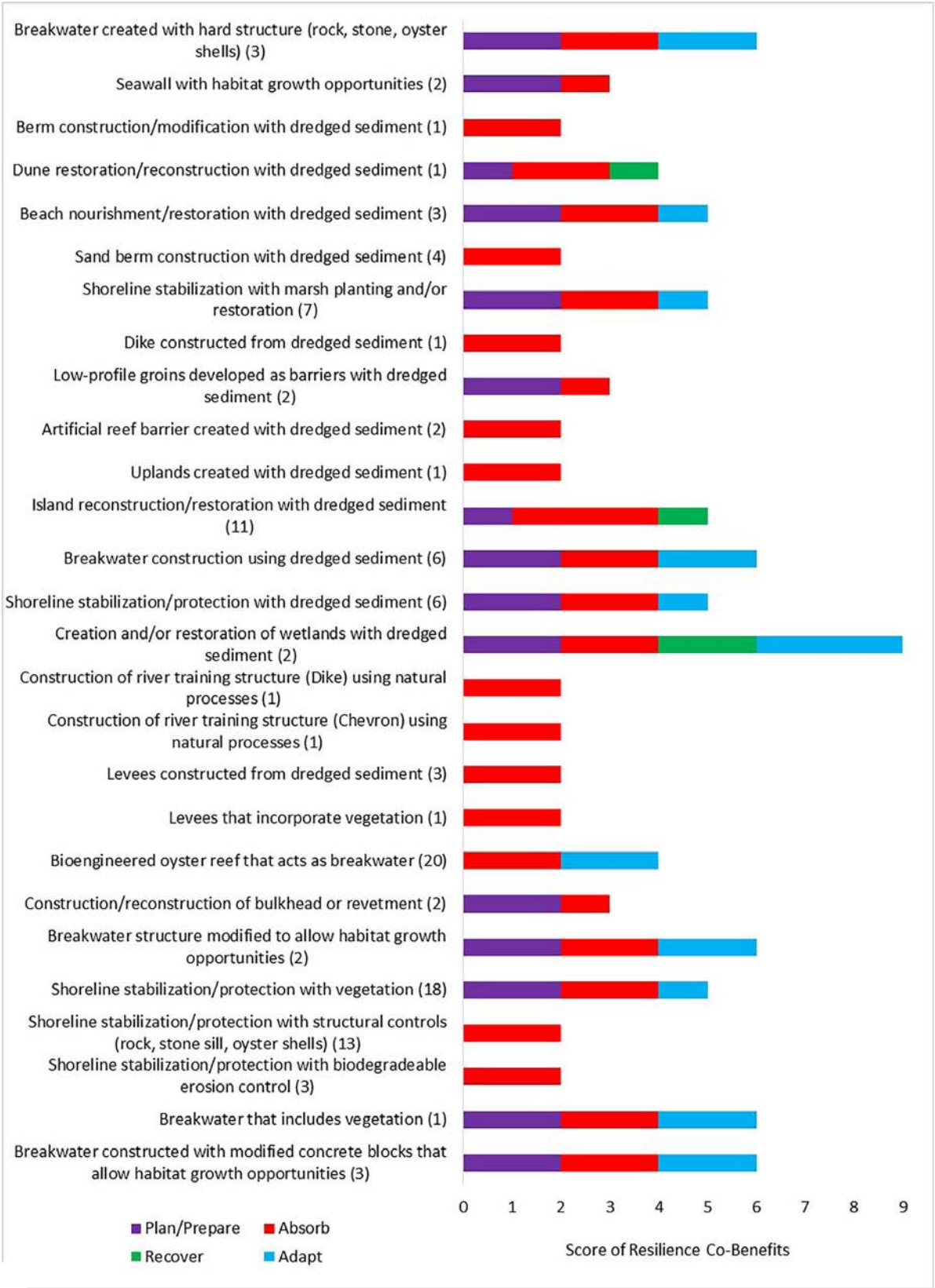

FIGURE 1 | Resilience scores of EWN features types. Number in parentheses indicates how many projects were classified as being of that feature type.

TABLE 1 | Resilience Indicators [adapted from Cunniff and Schwartz (2015)].

Resilience category	Indicators
Plan/Prepare	• Shoreline and/or sediment stabilization • Enhance shoreline accretion • Decrease shoreline erosion/mitigate shoreline retreat
Absorb	• Wave attenuation and/or dissipation • Protect and reduce erosion from storms and rising tides • Wind speed reductions due to windbreaks or shelter belts
Recover	• Promotes self-recovery after hazard event • Able to recover with minimal intervention • Timeframe of recovery is within expected time frame of next hazard
Adapt	• Adaptability to changing community needs • Self-adapt to various hazards • Enhance likelihood of landform evolution naturally

TABLE 2 | USACE business line indicators.

USACE business line	Indicators
Navigation Management	• Beneficial use of dredged sediment • Structures that adjust hydraulic flow for improved waterway navigation • Reducing the need for dredging in the future
Flood Management and Coastal Storm Risk Reduction	• Conventional and nature-based structures that attenuate wave energy • Barriers or buffers to prevent water intrusion • Development or restoration of shorelines • Shoreline erosion control
Environmental Restoration	• New vegetated areas added and/or previously vegetated areas restored • Supports the development of aquatic wildlife habitat • Construction and/or restoration of land masses

with dredged sediment; island reconstruction/restoration with dredged sediment; and creation and/or restoration of wetlands with dredged sediment. All 27 feature types had some indication of ability to absorb shocks whereas 15 met indicators for the ability to plan/prepare and 11 had indicators of being able to adapt.

A pairwise comparison between each of the indicators of USACE business lines and indicators of resilience, as shown in **Figure 2**, illustrates how many EWN feature types achieve a specific USACE civil works objective and contribute to resilience, as it was assessed in this study. The graph sums the number of resilience benefits that can be attributed to features that have an indicator of a business line. Each feature can have up to 12 "points," as that is the number of resilience indicators used in the assessment rubric. The results show that projects that incorporated beneficial use of dredged sediment scored highest in the resilience assessment. Projects that employed structures that attenuate wave energy and projects that constructed or restored land masses scored the second and third highest in the resilience scoring, respectively. The pairwise comparison indicates where there are opportunities to use civil work projects to achieve the types of benefits that comprise the resilience assessment.

DISCUSSION AND CONCLUSION

The connection between EWN and resilience, in both the engineering and ecological sense, is intuitive to some extent, but is in need of a more formal connection between management and outcomes as well as a method for enumeration. The challenge of drawing clear links between the two lies as much with the indeterminacy of resilience as a concept (Kurth et al., 2018) as with the diverse and growing experience of EWN practitioners. A solution lies partly in establishing appropriate performance metrics and associated monitoring schemes to establish the relative success of EWN. It is important to note, however, that a lack of a formal accounting process to measure the connection between EWN and resilience should not stifle efforts to maximize the co-benefits of USACE civil works projects, which have a rich history of success (Bridges et al., 2018). Progress in ecosystem management and engineering is often achieved through learning-by-doing and adaptive strategies (Walters and Holling, 1990).

Questions remain about the extent to which or under what circumstances EWN projects might outperform more traditional coastal engineering approaches. The prospect of features that can recover from disturbances and adapt to better survive future disturbances with minimal or no intervention is compelling particularly in comparison to conventional infrastructure, which has little to no capacity to do so. Both have thresholds beyond which they cannot perform as intended and a tradeoff likely exists between the capacity to perform one function (e.g., be robust to a high energy storm) with the capacity to perform another (e.g., regenerate and migrate). Formally conducting a tradeoff analysis will require more data about how coastal features perform under stress and shocks. Questions that arose during this project were ones such as: what level of disturbance would permanently undermine the self-healing capability of an engineered natural feature, at least to return to the intended structure and function? And for how long does a nature-based feature need to be managed before it is fully functional and self-sustaining? Nesshöver et al. (2017) offer some considerations to maximize the success and utility of nature-based solutions and accept certain realities, which are useful for confronting the questions we raise. They suggest that implementation should include provisions for knowledge creation and concurrent social and technical innovation, as well as clear definition of success criteria and target objectives within the multifunctional role of nature, among others.

The demands that resilience, as an objective, place on consequent management efforts are numerous; resilience arises from systems that possess several capabilities, which cannot realistically be performed by singular components. EWN features may be powerful additions to a portfolio of system components that enhance resilience. An example would be complementary combinations of approaches that utilize conventional infrastructure along with restored or created natural infrastructure such as a salt marsh or oyster reef (e.g., Toft et al., 2014). Disaggregating the capabilities that can be fulfilled by EWN projects may help capture this reality and allow these projects to enter into the realm of resilience assessment. For example, the Resilience Matrix is a framework proposed by

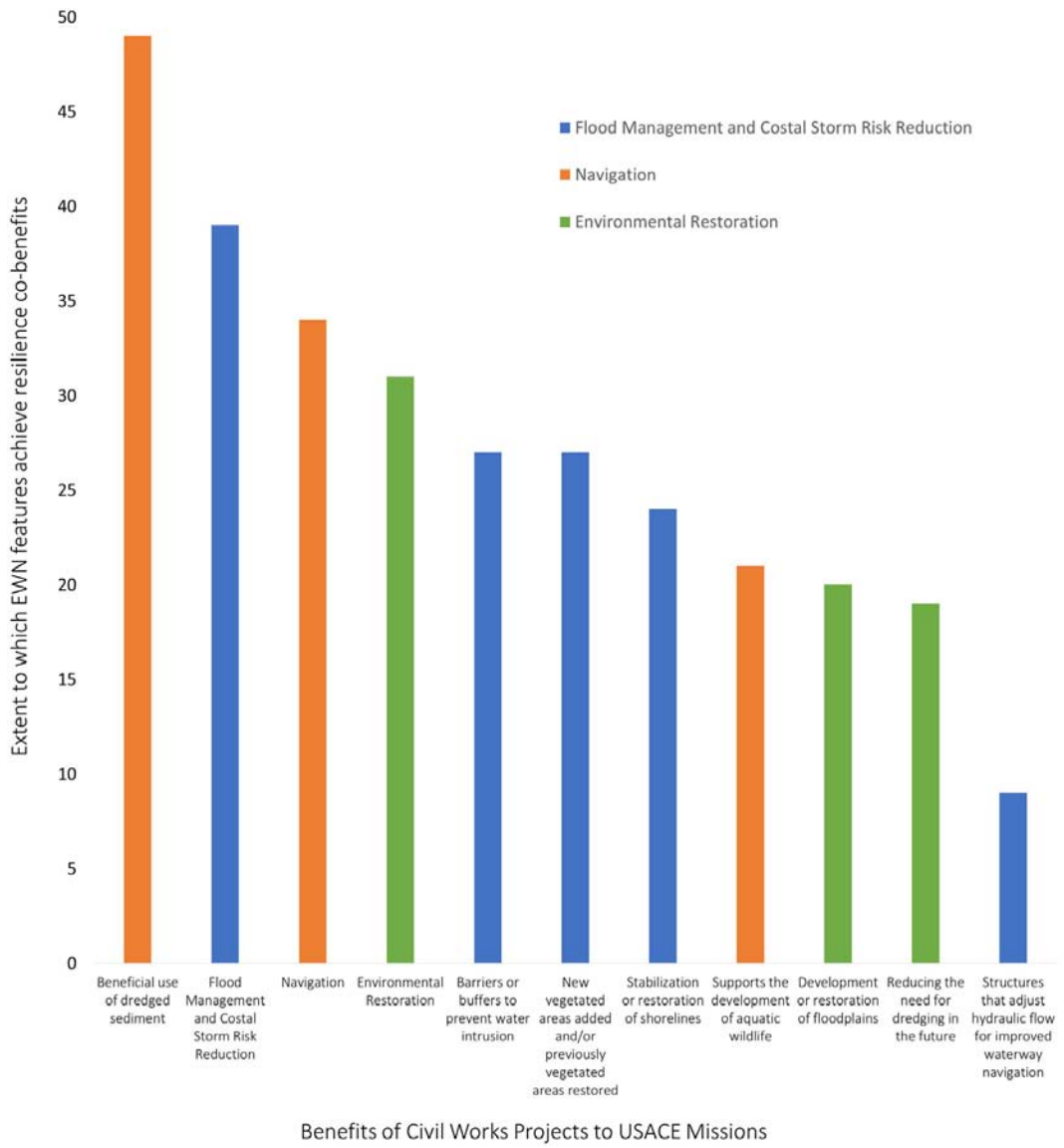

FIGURE 2 | Pairwise comparison of features with resilience benefits by business line indicator.

Linkov et al. (2013) and demonstrated by Fox-Lent et al. (2015) that structures the capabilities of a system that support it to maintain its performance quality despite stressors and shocks. Resilience assessment of this kind would place EWN projects alongside other elements that act in tandem to sustain a system. A formal accounting method to assess how EWN projects contribute to a system's ability to prepare, respond, absorb, and adapt to different hazards would improve the enumeration of the benefits that can be derived from these projects and improve decision making about enhancing the resilience of coastal systems.

This paper provides a critical look at the role that EWN projects can serve in potentially enhancing the resilience of communities via coastal ecosystems. In the absence of consistent project documentation, in part due to varied nature of EWN project types and monitoring data, a qualitative resilience assessment rubric was developed. However, as with many *ex ante* assessments, it is difficult to know if projects possess the abilities as they are assessed (i.e., they have not been put to the test or if tested, have not been documented).

Some important considerations are raised where the primary intention of establishing and restoring ecosystems is the creation of resilience co-benefits for adjacent communities and built infrastructure. Some are that resilient ecosystems naturally fluctuate to states that might deliver less or different benefits than that of the original state; natural recovery of ecosystems from disturbance takes place on vastly different time scales than is ideal for the intended object of their protection; and that successful establishment of healthy ecosystems can be compromised by nearby human disturbances. In general, a better understanding

of the coupled feedback loops between human and ecological coastal systems would be informative for maximizing benefits for both. For example, the ability of coastal ecosystems to buffer human systems from the impact of coastal processes may be dependent on the human systems managing the level of stress they place on ecosystems so that thresholds of what they can endure are not exceeded. Stated more simply, conserving and enhancing the natural system can support the resilience of coastal communities.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

MK and RA identified the research need, conceived of the research design, and wrote the manuscript. RA carried out the analysis. IL supervised the project. BS provided the critical feedback. TB contributed to framing.

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