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RESEARCH ARTICLE

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Spatial patterns of meadow sensitivities to interannual climate variability in the Sierra Nevada

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Abstract

Conservation of montane meadows is a high priority for land and water managers given their critical role in buffering the effects of climate variability and their vulnerability to increasing temperatures and evaporative demands. Recent advances in cloud computing have provided new opportunities to examine ecological responses to climate variability over the past few decades and at large spatial scales. In this study, we characterized the sensitivities (magnitude and direction of the slope) of meadow vegetation responses to interannual variations in climate. We calculated sensitivity as the regression slope between a 31-year (1985–2016) time series of Landsat-derived vegetation indices characterizing late-season vegetation vigour and water balance variables from the Basin Characterization Model. We identified April 1 snowpack as the climate variable the majority of meadows were most sensitive to. We assessed how vegetation sensitivities to snowpack varied with hydrogeomorphic context (e.g., climate, geology, soils, watershed geometry, and land cover) across the Sierra Nevada mountain range using factor analysis to reduce the dimensionality of the hydrogeomorphic data and multiple linear regression to model sensitivity responses. We found that meadow sensitivities to snowpack varied with long-term average meadow climate, indicators of watershed subsurface water storage capacity, and indicators of meadow vegetation composition. Alpine and subalpine meadows with high average annual precipitation but limited catchment subsurface storage exhibited the largest sensitivities. Our results provide a novel regional perspective on spatial patterns of meadow sensitivities to climate variability and the landscape-scale hydrogeomorphic factors that influence late-season water availability in meadow ecosystems in the Sierra Nevada.

KEYWORDS

climate variability, hydrogeomorphic context, meadows, Sierra Nevada, vegetation sensitivity

1 | INTRODUCTION

In the Sierra Nevada mountain range of California and Nevada, montane meadows are considered to be among the most vulnerable ecosystems to changing climate (Hauptfeld, Kershner, & Feifel, 2014). Climate influences meadows directly through the timing and amount of precipitation and evapotranspiration (ET), which modifies the position of the water table, and indirectly through changes in vegetation, which can alter meadow hydrology based on differential patterns of water use among species (Darrouzet-Nardi, D'Antonio, & Dawson, 2006). Due to the relatively shallow groundwater systems that support many meadows in the Sierra Nevada, decreases in spring snowpack and an earlier snowmelt may limit the availability of late-season water, resulting in a loss of meadow area and a shift to upland/xeric dominated ecosystems (Drexler, Knifong, Tuil, Flint, & Flint, 2013). Meadows may also experience declines in surface and shallow groundwater availability over longer time periods as warmer temperatures and longer growing seasons lead to increased ET rates (Goulden & Bales, 2014).

Numerous studies suggest that the response of individual meadows to changing hydrology associated with climate and/or management activities depends on the hydrogeomorphology of the meadow and the landscape setting (e.g., Loheide & Gorelick, 2007; Lowry, Loheide, Moore, & Lundquist, 2011; Weixelman et al., 2011). At the landscape scale, watersheds with deeper soils and greater volumetric soil water storage capacity have the potential to sustain meadow and watershed-scale ET rates later into the summer where downslope transfers of water (i.e., interflow) supplement local sources (Lundquist & Loheide, 2011). The geomorphology of a watershed can also influence the relative importance of groundwater and surface water flow. For example, Vivoni, Di Benedetto, Grimaldi, and Eltahir (2008) showed that watersheds with a greater proportion of area at higher elevations (i.e., characterized by a convex hypsometric curve) produced more late-season runoff and had a greater groundwater component than watersheds with a greater proportion of area at lower elevations (i.e., concave hypsometric curve). In the Sierra Nevada, convex watersheds could have a similar response due to a combination of more snow accumulation at higher elevations and more potential for groundwater flow and storage, which may sustain meadows later into the season, even if the groundwater system is small. At the local scale, geology can influence the relative timing and amount of groundwater and surface water inputs into montane wetlands (Kitlasten & Fogg, 2015; Onda, Komatsu, Tsujimura, & Fujihara, 2001). For example, permeable fractured volcanic and/or metamorphic rocks (typical of the Cascades) can transmit and store more water than impermeable crystalline intrusive rocks (typical of the Sierra Nevada), resulting in differential long-term responses to climate change (Drexler et al., 2013). Meadow site characteristics such as soil hydraulic properties, local climate, surface water availability from direct snowmelt or streamflow, and hillslope factors that influence lateral groundwater flow further influence meadow hydrology and vegetation characteristics (Loheide et al., 2009; Lowry, Deems, Loheide, & Lundquist, 2010).

Although the influence of hydrogeomorphic (HGM) controls on meadow responses to changing hydrology is well documented at local scales, the influence of these controls—and the degree to which existing spatial datasets sufficiently capture important variation in these controls—is not well documented at landscape to regional scales. Identifying generalizable patterns in meadow response to climate variability using landscape-scale predictors would allow managers to better anticipate meadow trajectories and persistence in response to climate variability and change. Landsat satellite imagery has proven to be an effective and efficient data source for monitoring key ecological attributes of meadows and riparian systems over extensive areas and time periods (Ager & Owens, 2004; Cartwright & Johnson, 2018; Cohen & Goward, 2004), including above-ground biomass, which relates to vegetation structure, function and composition, and vegetation water content. Recent advances in cloud computing (Gorelick et al., 2017) now permit efficient application of algorithms across the Landsat satellite image archive for long-term monitoring of groundwater dependent ecosystems with respect to climate and management (Dauwalter, Fesenmyer, Miller, & Porter, 2018; Hausner et al., 2018; Huntington et al., 2017).

In this context, our principal research objectives were to characterize (a) the magnitude and direction of meadow vegetation responses to interannual variations in climate and water balance variables and (2) how these responses vary in accordance with HGM contexts (e.g., climate, geology, elevation, topographic position, soils, and watershed geometry) across the Sierra Nevada. To accomplish these objectives, we developed a 31-year time series (1985–2016) of paired climate and Landsat data for 8,106 meadows in the study area and analysed the sensitivity of late-season vegetation vigour to contemporary variation in climate.

2 | METHODS

Our analysis involved several steps (Figure 1), including (1) meadow delineation and filtering, (2) calculation of annual vegetation and water balance metrics, (3) assessing sensitivities as the slope of the relationship between vegetation and water balance metrics, (4) deriving a suite of HGM predictor variables hypothesized to influence sensitivity, (5) reducing the dimensionality of HGM predictor variables, and (6) assessing the influence of HGM predictors on patterns of sensitivity.

2.1 | Study area

Our study area is focused on meadows of the Sierra Nevada Range of California and Nevada, USA, but extends to meadows in portions of adjacent ecoregions, namely, the Southern Cascades and Modoc Plateau at the northern extent of the study area, as well as the Northwestern Basin and Range, Mono, and Sierra Nevada Foothills (Figure 2a; Cleland et al., 2007). We hereafter refer to the study area as the Sierra Nevada, given that the vast majority of meadows occur in this range. The Sierra Nevada extends approximately 650 km from north to south, with elevations ranging from 305 m at its base in California's Central Valley to 4,421 m at the peak of Mount Whitney. The range is influenced by California's Mediterranean climate, with mild summer temperatures and minimal summer precipitation. In colder months, the western slope receives substantial precipitation; most of which falls as snow above 1,800 m, whereas most of the eastern slope is subject to rain shadow effects and receives very little precipitation (Schoenherr, 2017). The western slope is dominantly forested, but vegetation types range from shrub and chaparral in the foothills to subalpine forest and alpine meadow communities at higher elevations (Schoenherr, 2017; U.S. Geological Survey Gap Analysis

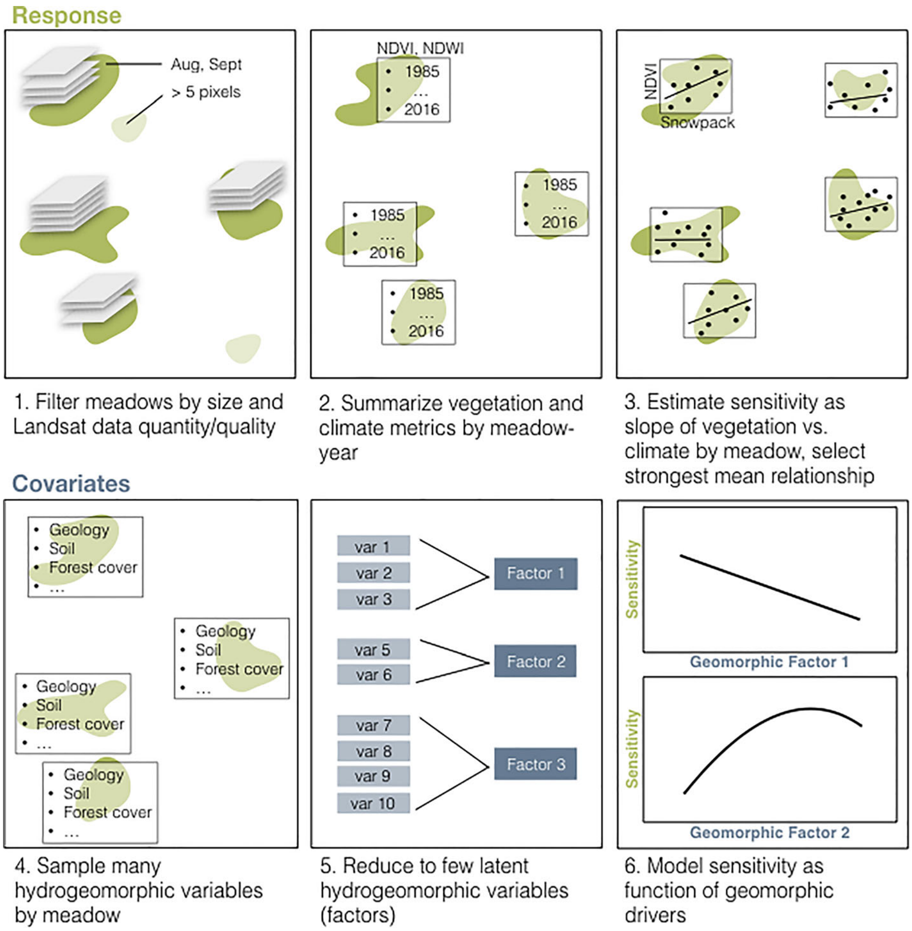


FIGURE 1 Outline of methodological steps taken to analyse spatial patterns of meadow sensitivities to climate variability. See Sections 2.2–2.7 for details on each step

Program, 2011). Shrubland vegetation types adapted to drier conditions are more common on the eastern side of the range. The Sierra Nevada is primarily managed by the U.S. Forest Service (U.S. Geological Survey Gap Analysis Program, 2011, 2012), where some energy and mining development, agricultural land use, and biological harvesting occur, with localized urban development in areas outside the National Forest. Meadows are distributed throughout the study area and throughout the area's elevation range, on both east and west slopes, although they are most common in the central and southern portions of the Sierra Nevada (Figure 2a).

2.2 | Meadow delineation and filtering

Our study sample initially included a subset of 8,106 meadow polygons compiled by a variety of agencies and organizations working in the Sierra Nevada (UC Davis Center for Watershed Sciences & USDA Forest Service, 2017). Meadows in this dataset were identified and boundaries were digitized from high-resolution (1 m) National Agriculture Imagery Program imagery. We selected meadows that fully contained at least five Landsat image pixels (totalling ~0.4 ha or 1.0 ac) in order to retain as many meadows as possible for analysis while ensuring that (a) enough pixels were present to obtain reasonable averaged vegetation condition metrics across the meadow extent and (b) influence of cover types at the meadow periphery (e.g., conifer cover) was minimized when calculating meadow vegetation metrics (Figure 2c). Finally, we delineated each meadow's watershed (Kitlasten, Clark, & Evans, 2019). Digital elevation model raster cells (30 m) intersected by the meadow polygons were used to define the base of the watershed (i.e. “pour points”), and each meadow's watershed was mapped using ESRI Spatial Analyst hydrology tools and flow direction raster available as part of the National Hydrologic Dataset Plus data model (McKay et al., 2012).

2.3 | Vegetation metrics

For each meadow, we computed a 31-year time series (water years of 1985–2016) of the spatially averaged normalized difference vegetation index (NDVI) and normalized difference water index (NDWI) derived from all usable late summer (Aug–Sept) Landsat (5, 7, and 8) 30-m imagery (at-surface reflectance derived from the USGS precollection top-of-atmosphere reflectance following Tasumi, Allen, & Trezza, 2008) using the Google Earth Engine cloud computing platform (Gorelick et al., 2017). These indices provide a measure of vegetation vigour (an indicator of biomass production; Anderson & Hanson,

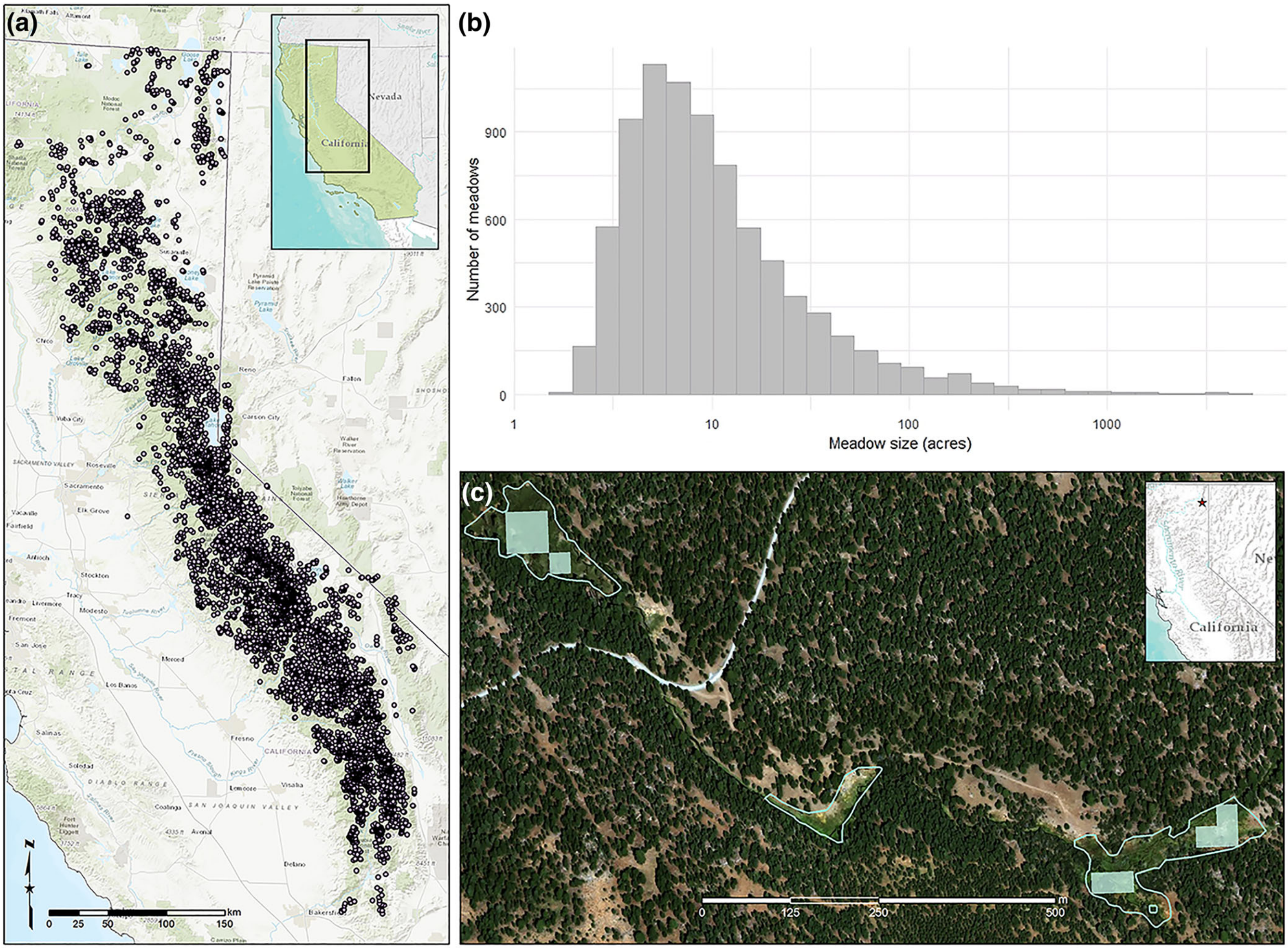


FIGURE 2 (a) Map of study area meadows included in the analysis and (b) distribution of meadow size (acres) and (c) filtering of meadows for analysis based on core area. Meadows (outlines) fully containing a minimum of 5 Landsat pixels (shaded) were retained; meadows with no pixel shading shown did not meet the minimum pixel number threshold and were excluded from analysis

1993) and vegetation water content (Gao, 1996), respectively. To ensure sufficient quality and quantity of data for analyses, we filtered these data to include only scenes with (a) 100% cloud- and shadow-free pixels (identified using Fmask; Zhu & Woodcock, 2014) for a given meadow, (b) only meadows with at least 300 scenes over the course of the time series, and (c) only meadows with at least one scene in both August and September in each of at least 30 years. For each meadow and year, we calculated and spatially averaged late-summer vegetation metrics that we expected to be highly sensitive to prior hydroclimatic conditions, namely, mean September NDVI and NDWI (Figure 3). All observations greater than two standard deviations below the historical mean value for September were removed prior to analysis in order to remove data influenced by snow cover (following Soulard, Albano, Villarreal, & Walker, 2016).

We chose to focus on the end of growing season because spring snowmelt provides the majority of groundwater recharge in this region that is later discharged during summer and fall (Huntington & Niswonger, 2012); therefore, comparing antecedent climate to late summer and early fall is ideal for assessing the persistence of baseflow conditions (McEvoy, Huntington, Abatzoglou, & Edwards, 2012), water availability, and associated meadow sensitivity. We selected September because it represents the timing when water table levels are at a minimum and because preliminary analyses indicated higher average vegetation index sensitivities in September relative to August.

2.4 | Climate and water balance sensitivity analysis

To assess sensitivity of meadow vegetation to climate conditions, we evaluated climate and water balance metrics from the California Basin Characterization Model (BCM; Flint & Flint, 2014); a 270-m resolution spatially downscaled version of the Parameter-elevation Relationships on Independent Slopes Model (Daly et al., 2008). Monthly resolution spatial means of multiple climate and water balance metrics for meadows were calculated from BCM data using the R geoknife tool (Read et al., 2015) and summarized by water year (Table 1). Multiyear (2–5 year) sums were also calculated for snowpack and potential ET metrics to assess lagged sensitivities of vegetation to cumulative-year water availability and evaporative demand.

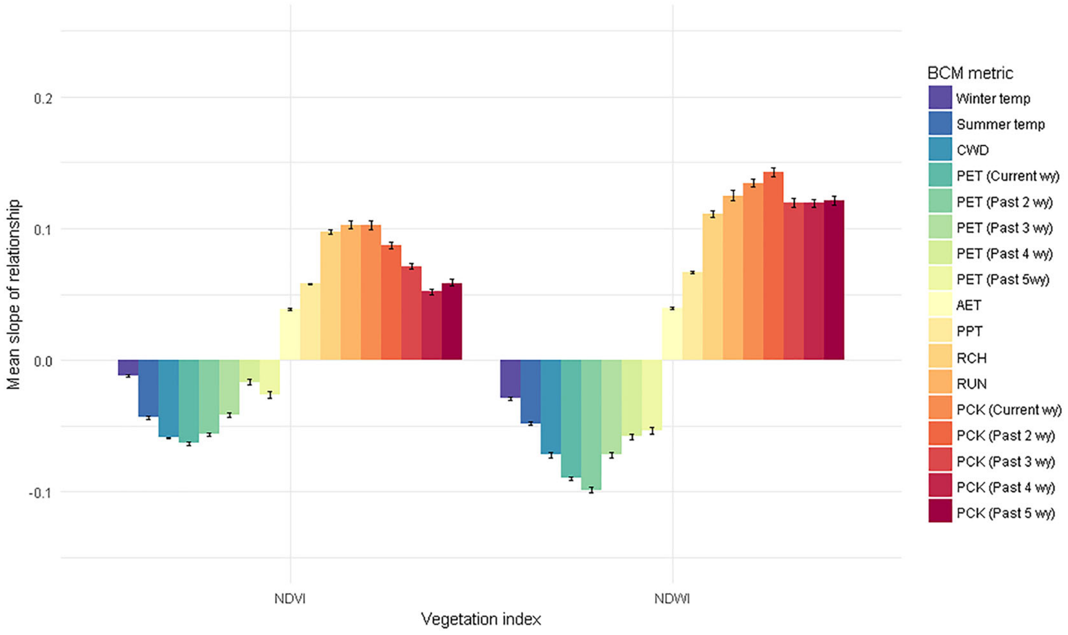


FIGURE 3 Comparison of potential sensitivity metrics based on the slope of the relationship between September vegetation indices (NDVI and NDWI) and water balance metrics (climatic water deficit [CWD], potential and actual evapotranspiration [PET and AET], precipitation [PPT], recharge [RCH], runoff [RUN], and April 1 snowpack [PCK]) from the Basin Characterization Model. Error bars represent 95% confidence intervals

TABLE 1 Annual (by water year) climate and water balance metrics from the California Basin Characterization Model to which late-summer meadow vegetation sensitivity was evaluated

Variable	Description
Actual evapotranspiration (ET)	Amount of water that evaporates from the surface and is transpired by plants
Climatic water deficit	Total evaporative demand that exceeds available water
Potential ET[a]	Total evaporative demand for well-watered and stress-free conditions
Precipitation	Total precipitation (rain or snow)
Recharge	Amount of water that penetrates below the root zone
Runoff	Amount of water that becomes stream flow
April 1 Snowpack[a]	Amount of water as snow water equivalent on April 1
Summer/winter temperature	Average temperature for winter (Oct–Mar) and summer (Apr–Sep)

[a]Multiyear (2–5 years) sums were also calculated to assess lagged responses.

We quantified meadow sensitivity to climate (and associated water balance) as the slope of the relationship between BCM climate and water balance metrics and vegetation indices in order to capture the magnitude of changes in vegetation condition in response to climate. Although slope alone does not fully capture how tightly vegetation characteristics are coupled (correlated) with climate conditions, we confirmed that there were no meadows in which the slope of the relationship between vegetation and climate was high despite the correlation being low (Figure S1). We estimated nonparametric slopes for each meadow from median-based linear models using the Siegel repeated medians method with the "mblm" package in R (Komsta, 2013). Median-based slope estimates were similar to those from ordinary least-squares regression models (r = .87–.96) but are far more robust to outliers (Siegel, 1982). We then selected the BCM metric with the highest mean slope across all meadows for both NDVI and NDWI as the metric best able to detect a response of meadow vegetation to climate for the entire study area.

2.5 | Hydrogeomorphic variables

Initial results from the climate and water balance sensitivity analysis indicated that on average, the largest sensitivities (i.e., slopes) of meadow vegetation indices were driven by interannual variability in April 1 snowpack (see Section 3.2; hereafter referred to simply as snowpack). Given these results, in addition to the known importance of snowpack to meadow structure and function (Arnold, Ghezzehei, & Berhe, 2014; Lowry et al., 2010; Lowry et al., 2011) and climate projections indicating reductions in late-season snowpack in the coming decades (Dettinger et al., 2018), we focused on the vegetation–snowpack relationship as the response variable of interest in our HGM context analysis. In order to understand the relative importance of meadow HGM context in driving sensitivity of meadow vegetation to snowpack variability, we modelled this sensitivity metric as a function of a suite of landscape variables using multiple regression. We derived several HGM context attributes that have been hypothesized to influence meadow vegetation sensitivity to climate conditions at both meadow and watershed scales (Table 2 and Figure S5). In addition, we included two management-related variables: the degree of human modification (Theobald, 2013; Theobald et al., 2016) and the fire regime departure classification (USDA Forest Service, 2011) for each watershed. The human modification metric was summarized for both meadows and watersheds. It provides a generalized characterization of both the areal extent and intensity of five main types (and 11 subtypes) of human development, including residential and commercial development, agriculture (including permitted livestock numbers), energy production and mining, transportation and service corridors, and biological harvesting; any of which may affect surface and/or groundwater influences on the meadow due to diversion of water and/or landscape alterations that affect natural hydrologic processes. The fire return interval departure class identifies the difference between current and presettlement fire frequencies. Locations within the study area with decreased fire frequency may have higher tree density, fuel loads, and water use and therefore may be less resilient to fire and potentially drought.

2.6 | Factor analysis of hydrogeomorphic variables

We reduced the HGM variable set to a smaller number of "latent" variables using factor analysis (FA; Thurstone, 1931) due to the large number of relevant variables; many of which were closely related (and correlated) to one another. This analysis is commonly used in social science applications in which latent variables of interest cannot be directly measured (e.g., depression) and are instead mathematically inferred from other observed variables (e.g., questionnaire responses regarding appetite and social engagement). Our aim in performing FA in this context was not only dimension reduction to obtain a more workable number of independent variables that are orthogonal (i.e., not strongly correlated) to each other but also to identify more meaningful and information-rich representations of underlying drivers of meadow sensitivity.

We used the "fa" function in the psych package for R (Revelle, 2018) to perform FA. We included only continuous numeric variables in FA and determined the number of factors to retain based on the Kaiser criterion (factors with eigenvalues >1; Kaiser, 1960). After Manly (1994), we excluded variables with no factor loadings >0.4 and then reran the analysis based on this reduced variable set. Only meadows with complete data for all HGM variables of interest could be included in FA; those with missing values were excluded from subsequent analyses. Assumptions critical to the suitability of the data for FA were met (Kaiser-Meyer-Olkin Measure of sampling adequacy >0.6, Bartlett's test of sphericity <0.05; Bartlett, 1937; Kaiser, 1981). However, several observed variables did not meet assumptions of normality (variables with skewed distributions conducive to transformation were log-transformed, but several others were heavily skewed and zero inflated). We therefore used the ordinary least squares FA method to find the minimum residual solution, which produces solutions very close to those of a maximum likelihood approach even when assumptions regarding the distributions of observed variables are violated (Revelle, 2018). We identified eight factors meeting the Kaiser criterion and used a varimax rotation to ease interpretation of factor loadings while preserving factor orthogonality.

2.7 | Hydrogeomorphic predictors of meadow sensitivity

To assess the relative importance of latent HGM variables as predictors of meadow sensitivity to climate, we fit multiple regression models, using robust model selection and multimodel inferential techniques (Burnham & Anderson, 2002). We used the slope-based snowpack sensitivity metric as our response variable (See section 3.2), after excluding outlier estimates based on Rosner's generalized extreme Studentized deviate test (Rosner, 1983). Predictor variables included latent HGM variables extracted from the FA and two categorical variables (HGM type and fire regime departure) that could not be integrated into the FA. Additionally, where continuous variables that we hypothesized to be strong drivers of sensitivity were excluded from the FA because they did not meet selection criteria described above (i.e., did not explain enough variability in the predictor space relative to the top factors), we included them as individual predictors. We used the MuMIn package for R (Bartón, 2016) to fit all possible subsets of a global model containing all categorical variables and linear and quadratic terms for all continuous variables. We then dropped quadratic terms and categorical variables that did not meet a significance threshold of $\alpha = .05$ in the model-averaged result, refit all subsets of the remaining global model, and then computed model-averaged regression coefficients, unconditional standard errors, and cumulative Akaike information criterion (AIC) weights of evidence (w+) as a measure of variable importance (Burnham & Anderson, 2002). We determined how well the final global model approximated the data by assessing Nagelkerke's adjusted r^2, a measure of variance explained after adjusting for the number of model terms that is consistent with maximum likelihood model estimation (Nagelkerke, 1991), as well as the difference between the global model AIC and that of a null model.

3 | RESULTS

3.1 | Meadow filtering

We identified 8,106 meadows out of 18,780 that fully contained at least 5 Landsat pixels for inclusion in our analysis. After filtering out meadows with insufficient quality or quantity of vegetation or climate data (388), our sensitivity analysis included a total of 243,922 meadow-year observations on 7,718 meadows, which ranged from 1.9 to 5,176 acres, with a mean area of 29.2 acres (Figure 2b). After removing meadows with missing HGM variable data (1,401) and outlier sensitivity estimates (seven for NDVI and 14 for NDWI), our HGM context analysis included 6,303 meadows for NDWI sensitivity and 6,310 meadows for NDVI sensitivity. Most meadows excluded due to missing data were in the southern Sierra Nevada and were missing soil available water capacity data.

TABLE 2 Landscape attributes hypothesized to influence meadow vegetation sensitivity to climate conditions

Variable	Description	Data source and resolution (if applicable)	Scale
Landform	Percent watershed classified as low (foot) slope or valley bottom (toe slope), cool slope, steep slope Rationale: low slope and valley landforms promote lateral groundwater flow that supports meadow vegetation, whereas steep slopes promote vertical flow. Cool slope aspects have longer duration snow storage.	Theobald, Harrison-Atlas, Monahan, & Albano (2015; 30 m)	W
Basin hypsometry/ curvature	Integral of watershed hypsometric curve Rationale: higher values of the integral of the hypsometric curve associated with a watershed indicate more convex form and suggests more water availability and more groundwater flow	Calculated in GIS based on 30-m digital elevation model (Strahler, 1952)	W
Meadow size/shape	Acreage, perimeter:area ratio of meadow Rationale: small acreage or high perimeter to area ratio meadows may be more sensitive to edge effects such as climate-induced upland vegetation encroachment	Calculated in GIS	M
Geology/ aquifer potential	Geology: percent watershed composed of extrusive igneous or metamorphic rock, percent watershed composed of intrusive igneous rock; Aquifer potential: percent watershed composed of geological types with unconsolidated geologic deposits. Rationale: watershed geologies with greater groundwater storage capacity and transmission may be less sensitive to climate variability.	Clynne & Muffler (2010; 1:50,000); Donnelly-Nolan (2010; 1:50,000); Elder & Reichert (2010; 1:4,000 to 1:250,000)	W
Soil	Mean available water capacity, (root zone, i.e., depth to root-growth-limiting soil horizon, and 0–150 cm) Rationale: meadows/watersheds with greater soil available water capacity have greater soil water storage and may be less sensitive to climate variability	Soil Survey Staff (2016; 1:12,000 to 1:63,360)	M, W
Hydro-geomorphic type	Meadow hydrogeomorphic type classification	UC Davis & USDA Forest Service (2017); Weixelman et al. (2011)	M
Watershed vegetation cover	Percent watershed with forest, herbaceous, barren cover; percent watershed with vegetation classified as dense; watershed average annual maximum greenness (eMODIS-based NDVI) Rationale: watersheds with greater forest cover have greater evapotranspiration (ET), which may confer high sensitivity, but high forest cover also indicates the presence of deep soils and associated potential water storage, as well as slower snowmelt, both of which may reduce sensitivity	Safford, van de Water, & Clark (2013); USGS EROS eMODIS (250 m)	W
Fire regime departure	Dominant direction of departure from historic fire return interval across watershed (more or less frequent fires) Rationale: watersheds with decreased fire frequency may be more sensitive to drought due to higher tree densities, fuel loading, and associated ET rates	Safford et al. (2013)	W
Historical climatology	Mean annual precipitation, potential ET, April 1 snowpack (1985–2016) Rationale: long term climate influences meadow hydrologic regime and associated vegetation types	Flint & Flint (2014; 270 m)	M, W
Meadow greenness	Mean late-season (Sept) NDVI (1986–2016) Rationale: long-term average greenness provides a generalized indicator of meadow biomass production and also relates to phenology and vegetation composition. Values greater than 0.6 typically indicate dense forest cover, while values in the 0.2–0.5 range indicate herbaceous and shrub cover.	NASA Landsat 5, 7–8 (30 m)	M
Human Modification	Mean degree of human modification Rationale: May affect surface or groundwater influences to the meadow due to diversion of water resources or landscape alterations that alter natural hydrologic processes, resulting in increased or decreased sensitivity	Theobald et al. (2016; 30 m); Theobald (2013; 30 m)	M, W

Abbreviations: M, meadow; W, watershed.

3.2 | Climate sensitivity

Overall, September NDWI displayed slightly higher average sensitivity to climate variables than September NDVI (Figure 3), but spatial patterns were similar (Figure 4). Vegetation indices were negatively related to (in increasing order of magnitude) seasonal temperature, climatic water deficit, and potential ET and were positively related to (in increasing order of magnitude) actual ET, precipitation, recharge, runoff, and April 1 snowpack (Figure 3). Temperature sensitivity was greater for summer (Apr–Sep) temperatures than for winter (Oct–Mar) temperatures. Although the NDVI–runoff relationship was not significantly different from that of the NDVI–snowpack relationship, April 1 snowpack had the highest average slope for both NDWI and NDVI (Figure 3), indicating that overall, this metric best captured sensitivity of meadow vegetation to climate. Sensitivity to snowpack also varied considerably among meadows (Figure S2), making it useful for assessing potential drivers of differences in sensitivity among meadows.

Spatial patterns of sensitivity were generally similar between the two groups of climate and water balance variables, representing atmospheric water demand (temperature, climatic water deficit, and potential ET) and water availability (precipitation, recharge, runoff, and April 1 snowpack; Figure 5). High sensitivities to April 1 snowpack (shown in dark pink/red) were more frequent and of higher magnitude than other variables, particularly at high elevations (Figure 5; see Figures S2–S3). Sensitivities to recharge and runoff showed similar patterns to snowpack and to each other, though higher sensitivities to recharge (runoff) were apparent in downslope (upslope) regions along the western slope of the Sierra Nevada. Of the evaporative demand variables, potential ET showed the most widespread high magnitude sensitivities, particularly in the San Joaquin basin northwest of Fresno and in the upper watersheds of the central Sierra Nevada, surrounding Lake Tahoe (Figures 4, 5). Although elevation was not explicitly included as a predictor variable in the HGM context analysis, in favour of more mechanistic variables such as historical climatology, elevation provides a useful point of comparison to existing watershed sensitivity studies and some climate sensitivities covaried closely with elevation. Snowpack and runoff sensitivities were generally low below 1,500- and 1,800-m elevation, respectively, and

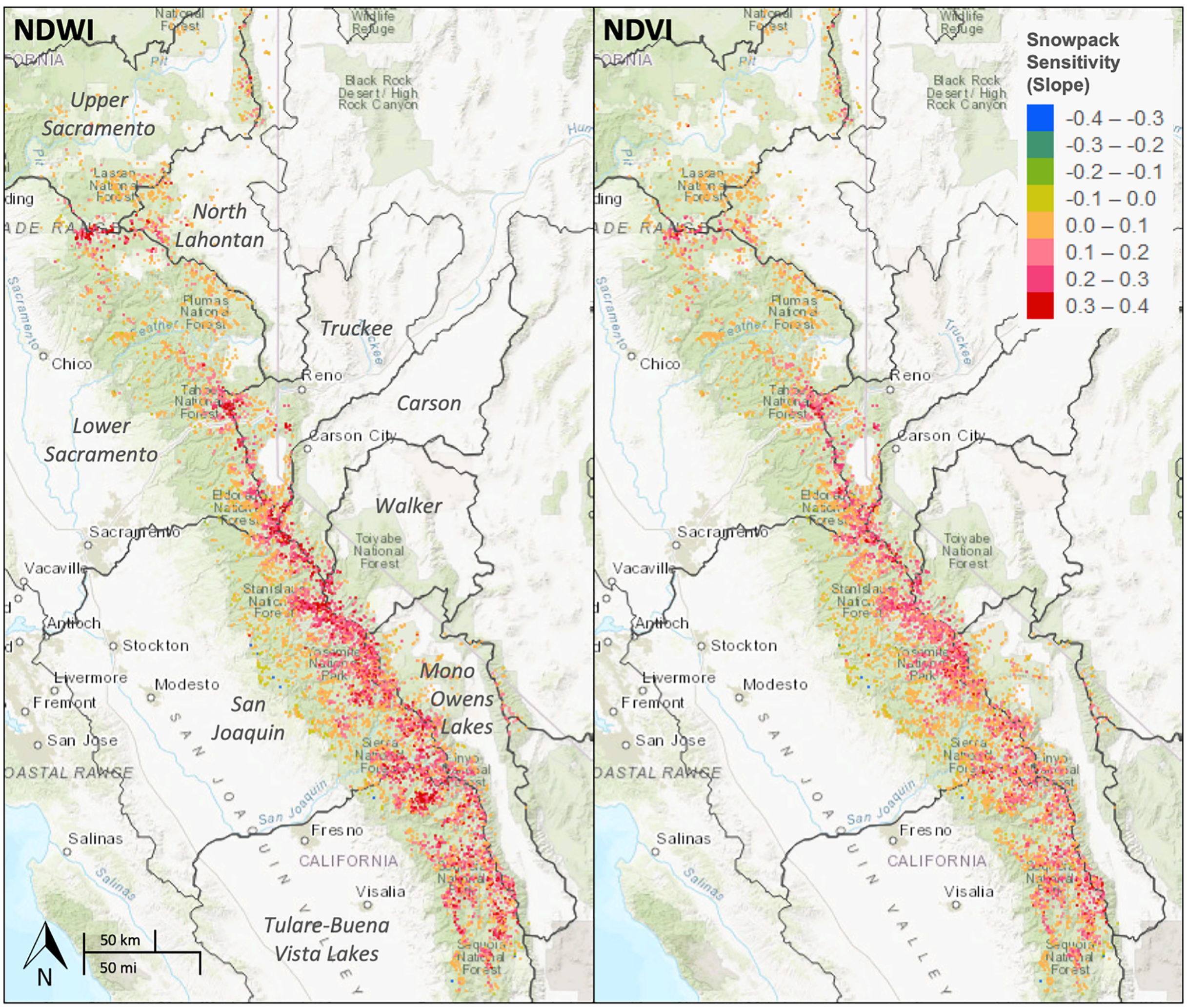


FIGURE 4 Mapped sensitivity metrics based on the slope of the relationship between September (a) NDWI and (b) NDVI and April 1 snowpack from the Basin Characterization Model. Outliers were excluded for the purpose of optimizing scaling. Grey lines indicate HUC-6 basins

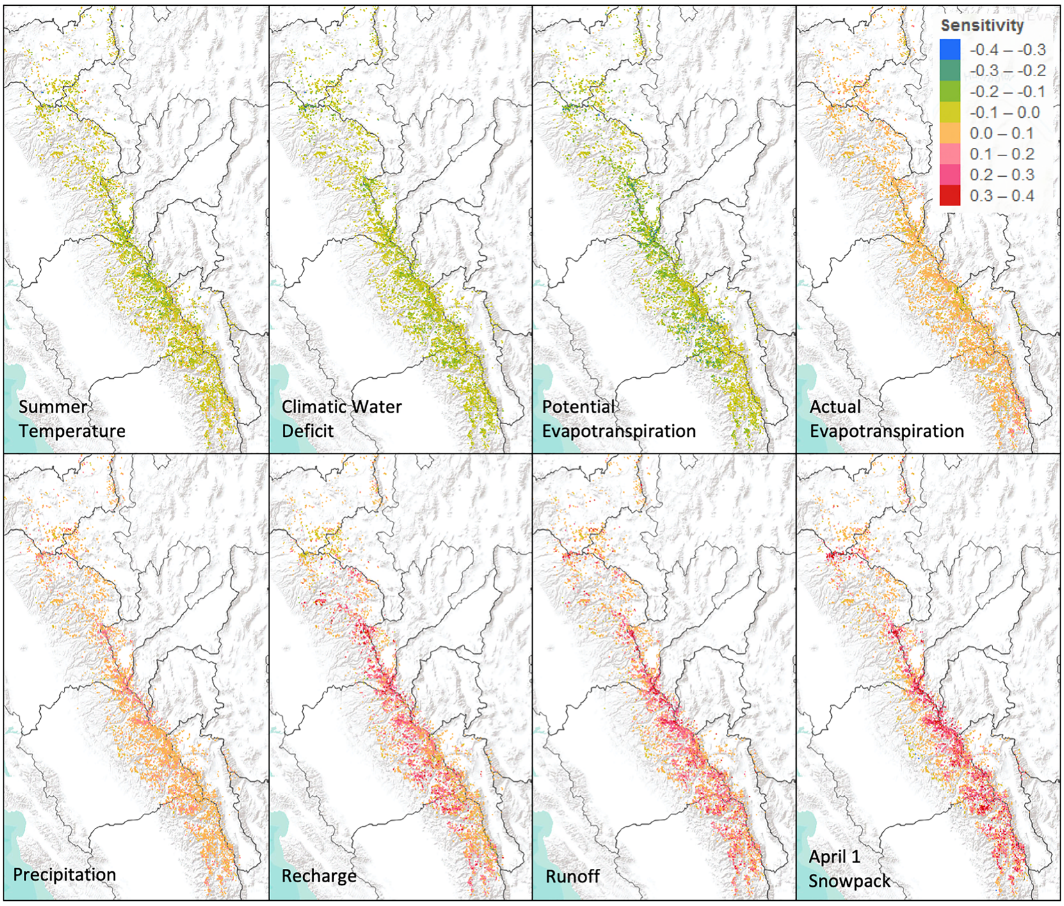


FIGURE 5 Spatial distribution of sensitivity metrics estimated from slopes of relationships between NDWI and eight Basin Characterization Model climate and water balance metrics. Higher magnitude slopes (either positive or negative) indicate higher sensitivity. Outliers were excluded for the purpose of optimizing scaling. NDVI sensitivity metrics showed very similar spatial patterns and thus are not shown. Histograms of the distributions for each metric can be found in Figure S2. Grey lines indicate HUC-6 basins. See Figure 4 for basin names

generally increased with elevation, with peak sensitivities occurring around 2,700 m and lower sensitivities at higher elevations. Recharge and potential ET sensitivities peaked around 2,200 m, with slightly lower sensitivities at lower and higher elevations (Figure S3).

Comparisons among multiyear metrics for sensitivity to potential ET and April 1 snowpack indicated that meadow NDVI was most sensitive to same-year climate conditions, whereas NDWI had high sensitivities to both same-year and cumulative climatic conditions over multiple years (Figure 3). Spatial patterns of NDWI sensitivities to multiyear cumulative snowpack (Figure S4) indicate that meadows in the far southern Sierra Nevada and in the Plumas National Forest were more sensitive to 5-year snowpack than to same-year snowpack.

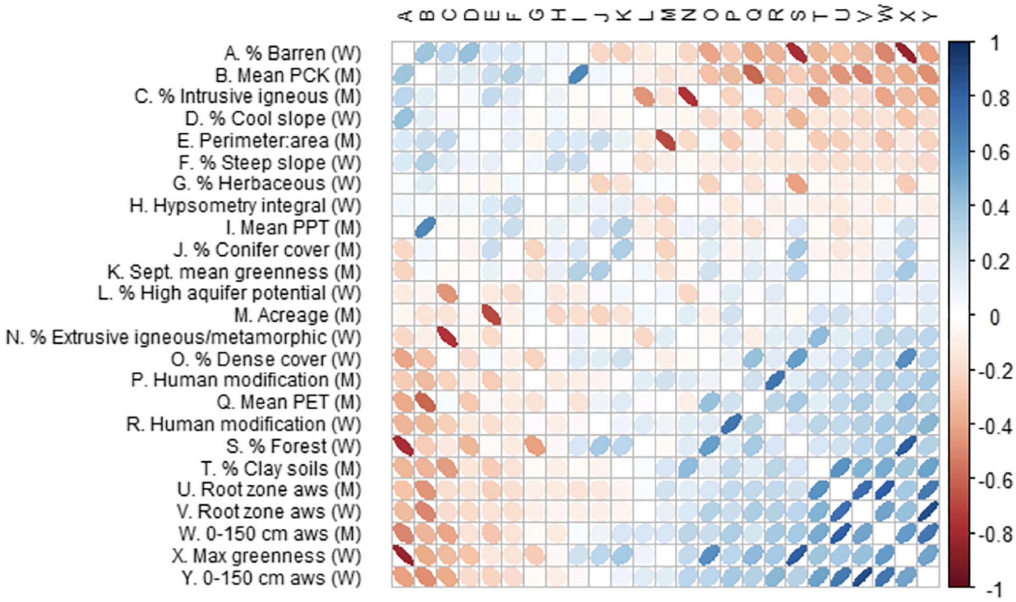
3.3 | Hydrogeomorphic Factor Analysis

Many of the HGM context variables were highly correlated with each other (i.e., $r > .5$; Figure 6a), justifying the use of FA. We identified eight factors, or latent variables, that together explain 76.2% of the variability among 25 retained observed variables. For ease of interpretation, we named these factors according to the measured variables that loaded most heavily on each (i.e., with loadings closest to ±1; Figure 6b). In order of proportion of the variance in measured variables explained, these factors included: "watershed forestedness," "meadow water storage," "geology," "meadow climate," "watershed water storage," "human modification," "meadow size," and "aquifer potential." Variables that were dropped from FA because they did not meet the loading threshold but were expected to be important in explaining sensitivity and thus were included as additional predictors in the regression analysis included 30-year mean meadow September greenness, watershed basin curvature (hypsometric integral), and watershed percent valley bottom (percent area classified as low slope and valley).

3.4 | Influence of hydrogeomorphic variables on meadow sensitivity

We obtained similar but not identical regression model results for NDVI and NDWI snowpack sensitivities; we therefore present both. Our final global model of NDWI-based meadow sensitivity (Table 3a) had an AIC value of 4,130 units below that of the null model and an adjusted r^2 of 0.484, indicating that it approximated the data reasonably well. All continuous predictors as well as categorical departure

(a)



(b)

	Watershed forestedness	Meadow water storage	Geology	Meadow climate	Watershed water storage	Human modification	Meadow size	Aquifer potential
A. % Barren (W)	-0.79	-0.16	-0.15	0.07	-0.06	-0.17	-0.11	-0.07
B. Mean PCK (M)	-0.30	-0.16	-0.07	0.89	-0.22	-0.17	-0.11	0.00
C. % Intrusive igneous (W)	-0.09	-0.11	-0.86	-0.02	-0.09	-0.13	-0.12	-0.43
E. Perimeter:area ratio (M)	-0.02	-0.11	-0.13	0.11	-0.04	-0.13	-0.79	-0.06
I. Mean PPT (M)	0.23	-0.03	0.04	0.78	0.00	-0.02	-0.14	-0.06
K. Sept mean greenness (M)	0.39	0.00	-0.03	0.16	-0.08	0.05	-0.14	0.06
L. % High aquifer potential (W)	0.03	0.04	0.01	-0.04	0.01	0.09	0.06	0.99
M. Acreage (M)	-0.07	0.08	0.05	-0.07	0.04	0.06	0.81	0.01
N. % Extrusive igneous/metamorphic (W)	0.07	0.09	0.95	0.05	0.07	0.06	0.10	-0.24
O. % Dense cover (W)	0.63	0.05	-0.07	-0.09	0.17	0.02	-0.09	0.00
P. Human modification (M)	0.11	0.13	0.09	-0.12	0.07	0.72	0.17	0.05
Q. Mean PET (M)	0.44	0.06	-0.12	-0.45	0.14	0.18	-0.05	-0.02
R. Human modification (W)	0.18	0.10	0.07	-0.08	0.15	0.90	0.04	0.06
S. % Forest (W)	0.85	0.09	0.07	0.03	0.08	0.02	0.01	-0.04
T. % Clay soils (M)	0.19	0.44	0.36	-0.12	0.19	0.19	0.14	-0.01
U. Root zone aws (M)	0.13	0.86	0.02	-0.17	0.40	0.11	0.13	-0.02
V. Root zone aws (W)	0.21	0.34	0.07	-0.17	0.87	0.12	0.05	-0.03
W. 0-150 cm aws (M)	0.32	0.80	0.20	-0.01	0.22	0.20	0.16	0.12
X. Maximum greenness (W)	0.92	0.18	0.19	0.00	0.13	0.18	0.04	0.03
Y. 0-150 cm aws (W)	0.28	0.38	0.20	-0.12	0.74	0.25	0.10	0.09

FIGURE 6 (a) Correlations among all measured meadow (M) and watershed (W) scale hydrogeomorphic variables and (b) loadings of each hydrogeomorphic variable on eight latent variables or factors (after excluding variables with no loadings >0.4; see Supporting Information for details). See Table 2 for variable descriptions. PET, potential evapotranspiration; PCK, April 1 snowpack; PPT, precipitation; aws, soil available water storage

from fire regime had AIC weights of evidence of 1.0 except aquifer potential (w+ = 0.72). Our final global model of NDVI-based sensitivity (Table 3b) had an AIC value of 3,613 units below that of the null model and an adjusted r^2 of .439, indicating that it also approximated the data reasonably well. Similarly, all predictor variables except aquifer potential (w+ = 0.97) had AIC weights of evidence of 1.0.

As indicated by the magnitudes of the regression coefficients, meadow climate and watershed forestedness showed the strongest associations with snowpack sensitivity, with progressively smaller magnitude responses to average meadow greenness, human modification, watershed water storage, meadow water storage, geology, basin curvature, meadow size, percent valley bottom, and fire regime departure (Table 3). Aquifer potential, percent cool slope, and HGM type variables were not significant (i.e., 95% confidence limits around the estimate included zero), and the latter, which was a categorical variable, was dropped from the analysis. The relative magnitude of coefficients and confidence limits of quadratic terms in the NDVI-based sensitivity model differed slightly in some cases from the NDWI-based model (Table 3), but overall patterns of all univariate relationships were similar (Figure 7). The most sensitive meadows had wetter climate, occurred in less forested watersheds, and had moderate long-term average meadow greenness (Figures 7a,b,h and 8). These meadows also had lower water storage capacity at both the watershed and meadow scales (Figure 7d,e). Meadows in watersheds with more extrusive igneous or metamorphic rock than intrusive igneous rock (Figure 7f) that have more convex basin curvature (Figure 7i) and with greater extent of valley bottom (foot slope) and low (toe slope) landforms (Figure 7h) were less sensitive. Smaller meadows with a low degree of human modification at the meadow and watershed scales tended to be more sensitive than those that have been

TABLE 3 Summary of final inferential models for meadow vegetation sensitivity to climate based on the relationship between (a) NDWI and (b) NDVI and snowpack

(a)	Term	Variable importance	Coefficient estimate	Adjusted SE	95% Lower CL	95% Upper CL
Intercept			0.160	0.003	0.154	0.167
Meadow climate	x	1.00	4.015	0.094	3.831	4.198
	x^2		−0.231	0.087	−0.400	−0.061
Watershed forestedness	x	1.00	−2.686	0.138	−2.957	−2.415
	x^2		−0.453	0.096	−0.641	−0.266
Human modification	x	1.00	−1.562	0.091	−1.741	−1.383
	x^2		0.280	0.086	0.111	0.449
Watershed water storage	x	1.00	−1.480	0.089	−1.655	−1.305
	x^2		0.197	0.093	0.015	0.380
Average meadow greenness	x	1.00	1.218	0.098	1.026	1.410
	x^2		−2.064	0.085	−2.231	−1.896
Meadow water storage	x	1.00	−0.802	0.093	−0.985	−0.620
	x^2		−0.253	0.092	−0.434	−0.072
Geology	x	1.00	−0.648	0.092	−0.827	−0.468
Basin curvature	x	1.00	−0.485	0.096	−0.673	−0.297
Meadow size	x	1.00	−0.347	0.091	−0.526	−0.168
Watershed fire regime	More frequent	1.00	−0.035	0.021	−0.075	0.005
	Less frequent		−0.036	0.004	−0.044	−0.028
	NA		−0.025	0.004	−0.033	−0.016
Watershed % valley bottom	x	0.97	−0.287	0.110	−0.502	−0.071
Aquifer potential	x	0.72	0.124	0.107	−0.087	0.334
Percent cool slope	x	0.28	0.010	0.051	−0.090	0.111
(b)						
Intercept			0.109	0.003	0.104	0.115
Meadow climate	x	1.00	3.062	0.074	2.917	3.207
	x^2		−0.731	0.069	−0.866	−0.596
Watershed forestedness	x	1.00	−2.383	0.111	−2.599	−2.166
	x^2		−0.477	0.076	−0.627	−0.328
Average meadow greenness	x	1.00	0.429	0.079	0.275	0.583
	x^2		−1.688	0.068	−1.822	−1.554
Human modification	x	1.00	−0.969	0.071	−1.108	−0.830
Watershed water storage	x	1.00	−0.907	0.069	−1.042	−0.773
Meadow water storage	x	1.00	−0.536	0.070	−0.673	−0.398
Geology	x	1.00	−0.473	0.073	−0.616	−0.330
Meadow size	x	1.00	−0.377	0.071	−0.516	−0.237
Watershed % valley bottom	x	0.99	−0.273	0.083	−0.435	−0.110
Watershed fire regime	More frequent	0.99	−0.020	0.016	−0.052	0.012
	Less frequent		−0.008	0.003	−0.014	−0.001
	NA		−0.012	0.004	−0.020	−0.005
Aquifer potential	x	0.97	0.200	0.078	0.047	0.353
Basin curvature	x	0.62	−0.080	0.087	−0.250	0.090
Percent cool slope	x	0.32	0.017	0.048	−0.077	0.112

Note. Variables with confidence intervals that span zero are indicated by grey shading.

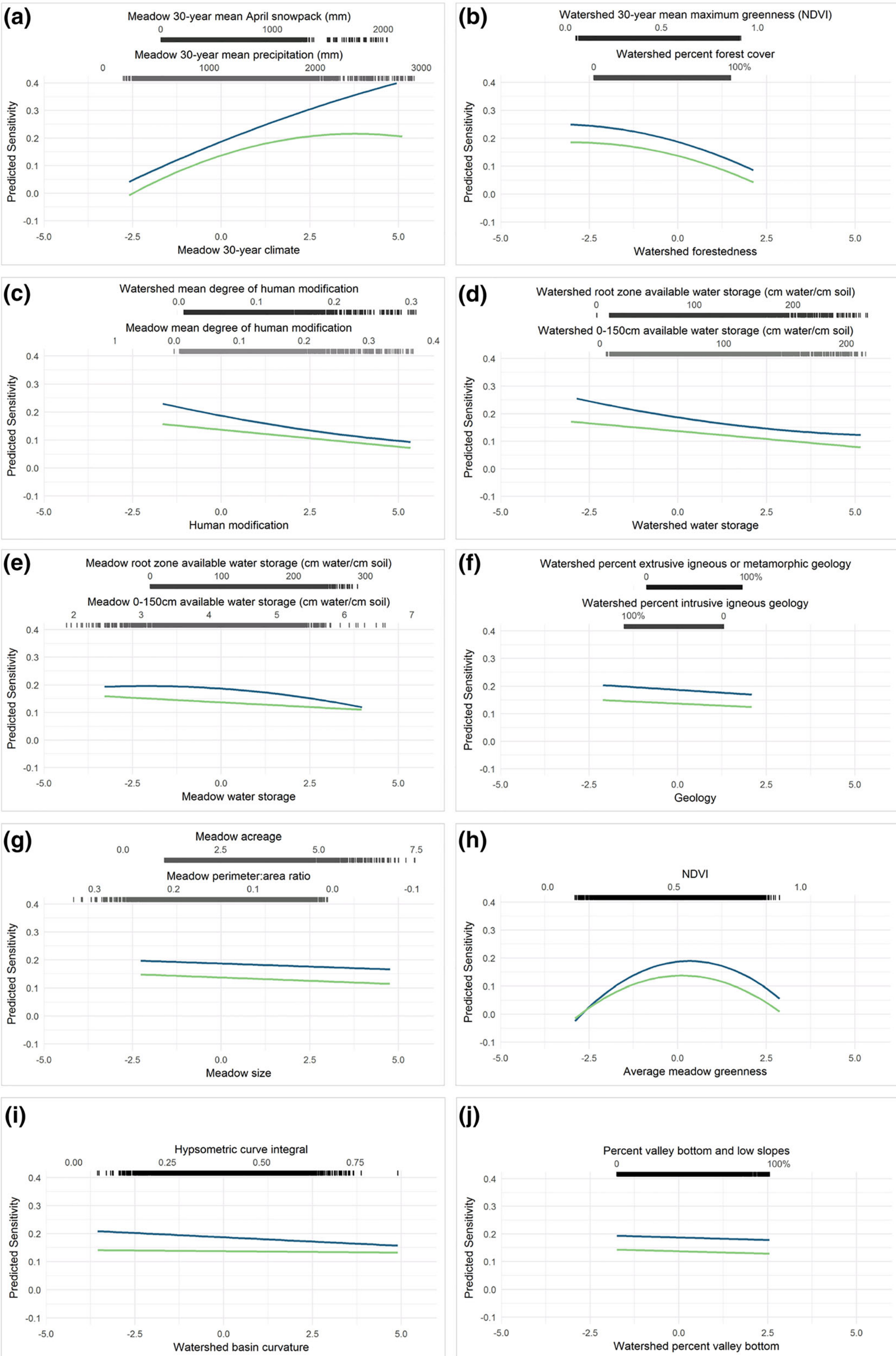


FIGURE 7 Model-predicted univariate relationships of meadow sensitivity based on NDWI (blue) and NDVI (green) with and model covariates when all other variables are held constant at their means, including latent attributes (factors; a–g) and additional continuous variables included in final inferential models (h–j). NDWI- and NDVI-based relationships are shown in blue and green, respectively. Rug plots (top) show the approximate distribution of original measured variables that loaded heavily on each factor as they relate to standardized factor score scales and are shaded according to their loading (darker = higher loading; a–g). In the case of additional variables included individually or original measurement scales in the case of additional variables included in inferential models (h–j), rug plots show original measurement scales as they relate to standardized plot scales

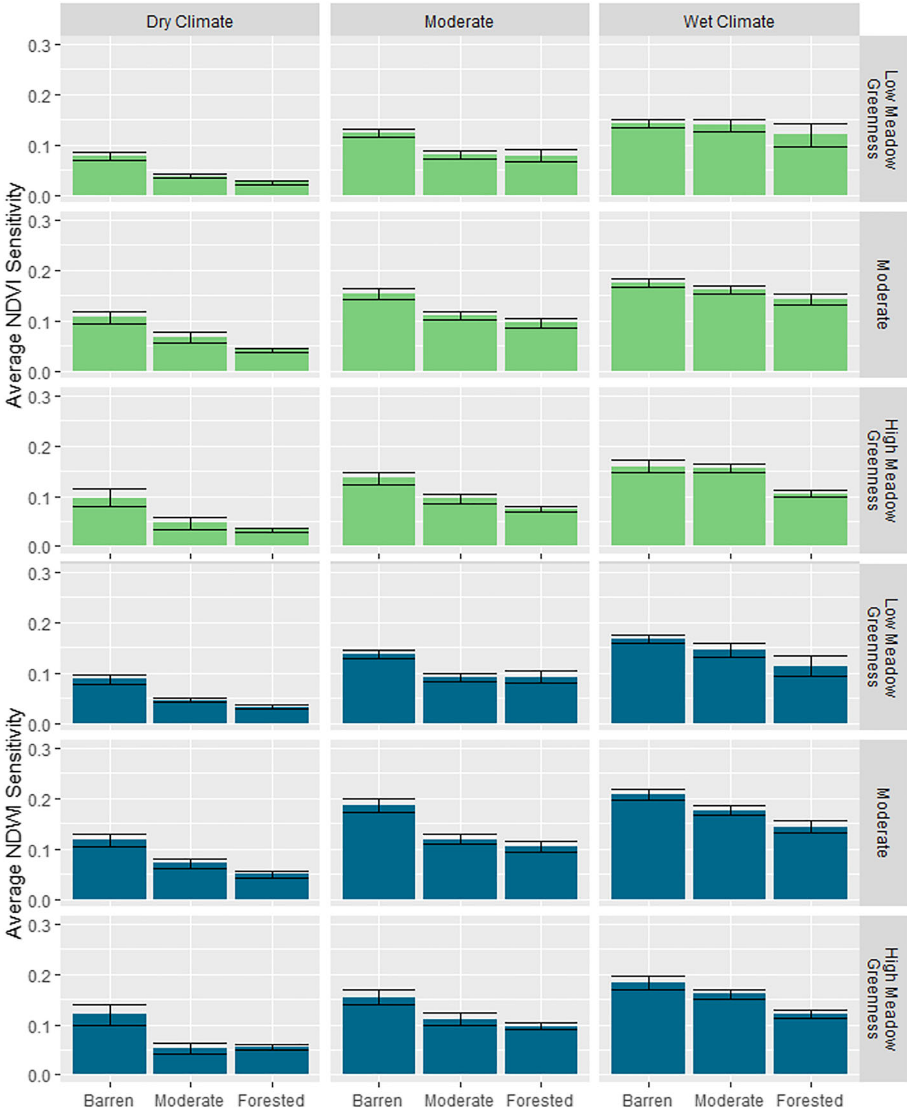


FIGURE 8 Relations between average meadow sensitivity based on NDWI (blue) and NDVI (green) and the three strongest predictor variables divided into three quantiles (tertiles), including long-term average meadow climate, watershed forestedness, and long-term average meadow greenness (<0.45 = low greenness, >0.6 = high greenness). Error bars indicate 95% confidence limits

modified, and differences among fire regime departure classes were minimal.

More specifically, NDWI-based sensitivity of meadow vegetation to meadow climate (i.e., water availability) was mostly linear, whereas NDVI-based sensitivity flattened and declined slightly at the highest mean levels of precipitation (>2 m/year) and snowpack (>1.25 m/year; Figure 7a). Both NDWI- and NDVI-based sensitivities exhibited a threshold-like relationship with watershed forestedness, in which sensitivity declined more sharply above approximately 25% watershed forest cover (Figure 7b). Meadows with intermediate mean greenness (~0.5–0.6) had the highest sensitivity according to both NDWI- and NDVI-based metrics (Figure 7h). Basin curvature (convexness) had a weaker relationship with NDVI-based sensitivity than with NDWI-based sensitivity (Figure 7i). All other relationships were approximately linear and very similar across both sensitivity metrics.

4 | DISCUSSION

4.1 | Climate sensitivity

Overall, meadow vegetation indices were most strongly related to derived metrics of water surplus and availability, including recharge, runoff, and snowpack (Figure 3). These indicate the added value of the BCM water balance variables beyond that provided by a simple measure of precipitation. We observed similar spatial patterns between NDVI and NDWI sensitivities, but NDWI sensitivities tended to be larger in magnitude (Figures 3, 4). Although NDVI and NDWI tend to be highly correlated, they are distinct and complementary measures of vegetation vigour: The former measures chlorophyll content, whereas the latter measures water within plant tissue (Gao, 1996). The fact that NDWI tended to be a more sensitive measure may be indicative of the fact that at the end of the water year, vegetation experiencing water stress (indicated by NDWI) may still not have begun to senesce (indicated by NDVI), even under water-stressed conditions (Gu, Brown, Verdin, & Wardlow, 2007).

NDWI was also more sensitive to multiyear snowpack than was NDVI, with some meadows even exhibiting higher sensitivities to cumulative year snowpacks than to same-year snowpack. This primarily occurred in the Kern River basin at the southernmost end of the Sierra Nevada and in the Feather River basin, at the northernmost end of the range. Although an analysis of HGM drivers related to multiyear sensitivities was outside the scope of this study, these two basins are notable in that they both contain a relatively large number of groundwater dependent ecosystems (Howard & Merrifield, 2010). Kern has some of the highest elevations and can retain snowpack for longer durations relative to other basins, whereas the Feather has the highest precipitation and most groundwater relative to other basins in the Sierra Nevada due to the presence of permeable volcanic geologies (Null, Viers, & Mount, 2010). Either of these factors may relate to the slower varying responses and higher groundwater dependencies observed in these regions.

We selected the September vegetation–snowpack relationship as our sensitivity metric given that this was the climate variable that most meadows in our study were most sensitive to, because snowpack is an important driver of meadow hydrology (Lowry et al., 2010), productivity, and nutrient fluxes (Arnold et al., 2014) and because April 1 snowpack is expected to be strongly affected by warming climate (Dettinger et al., 2018). Meadows with high sensitivity are those with late-season vegetation phenology (i.e., greenness and water content) that synchronizes closely with April 1 snow water equivalent in the same year, indicating a strong dependence on proximate snowmelt-derived water sources, which may include direct snowmelt, streamflow, or influxes from the surrounding hillslope (Lowry et al., 2010). Conversely, meadows with low sensitivity in September may lack significant annual snow cover (i.e., are at low elevations) or may have groundwater inputs that vary on longer than interannual timescales, resulting in end-of-season vegetation vigour that is less sensitive to interannual variations in snowpack. Indeed, many of the meadows exhibiting low September sensitivity to snowpack were located at lower elevations and in the northern portion of the study region (Figure 4), where precipitation occurs more commonly as rain, rather than snow, and where groundwater is influential over slower (i.e., decadal) varying timescales (Drexler et al., 2013), suggesting that multiyear lag effects may be more important than same-year precipitation or snowpack. Variations in sensitivity could also be due to a number of other factors, including human modifications or unmeasured landscape changes at the meadow or watershed scales that occurred over the course of the study.

Actual ET and vegetation indices such as NDVI are expected to be strongly and positively correlated, especially when vegetation indices are integrated over the entire season (Goulden et al., 2012); however, this relationship was quite weak relative to those with other water balance variables in our study (Figure 3). This may be attributed to the fact that the BCM simulates actual ET based on available water storage in the soil, including contributions from direct snowmelt (Flint, Flint, Thorne, & Boynton, 2013), but is not accounting for deep and/or shallow groundwater subsidies that allow vegetation to persist late in the season as is the case for most meadow ecosystems in our study. These results suggest that many of the meadows in this study depend on these groundwater subsidies, and that estimates of climatic water deficit and actual ET should be interpreted with caution in ecosystems where plant water use is not limited to what is available in the soil column. In the case of these systems, potential ET may provide a closer estimate of plant water use as the groundwater subsidy allows meadow vegetation productivity to more closely track atmospheric water demands.

4.2 | Hydrogeomorphic context analysis

We found that long-term climate, watershed forestedness, and average meadow greenness (an indicator of overall productivity and composition) were the best predictors of spatial variability of meadow sensitivity (Table 3 and Figure 7). Patterns associated with other predictor variables were more subtle; thus, we focus the bulk of our interpretation of results and associated inferences on these three predictors.

Meadow 30-year average climate, reflecting elevational, latitudinal, and rain-shadow-based gradients of water supply and evaporative demand, was the strongest predictor of sensitivity (Table 3 and Figure 7a). NDVI sensitivity peaked at locations where 30-year average precipitation amounts were about 200 cm and then declined at higher amounts, whereas NDWI increased linearly. The NDVI response reflects the transition from water to energy limitations on vegetation productivity at high elevations, similar to that observed for forest vegetation by Trujillo, Molotch, Goulden, Kelly, and Bales (2012). The more linear response of NDWI may be due to the fact that it is simply a measure of vegetation water content and thus less influenced by the energy limitations at high elevations that limit the photosynthetic response reflected by NDVI. Notably, snowpack sensitivity responses in our study were consistently high above about 2,100 m and peaked in the 2,500- to 2,700-m range (Figure S3). Projected snowpack losses in the Sierra Nevada by the end of century are expected to be greatest below 2,400 m (Dettinger et al., 2018), suggesting that those meadows at the highest elevations, though sensitive, may not be as vulnerable to changing climate due to reduced exposure to changes in snowpack, albeit earlier snowmelt and warmer temperatures will still result in increasing atmospheric water demands.

Watershed forestedness was the second strongest predictor of meadow sensitivity (Table 3 and Figure 7b), with meadows in watersheds that had higher percent forest cover, higher tree densities, and larger annual maximum greenness values consistently exhibiting lower sensitivities to interannual snowpack variability across climatic gradients from dry to wet (Figure 8). In contrast, meadows located in more barren watersheds characterized by granitic domes, shallow soils, and sparse vegetation cover, as is typical in many regions of the Sierra Nevada, exhibited higher sensitivities. Our interpretation of this result is that, at the Sierra-wide scale of our analysis, watershed attributes related to enhanced subsurface water storage capacity that have coevolved with (Jenny, 1941), and are potentially indicated by (*sensu* Stewart, 2013; Thompson, Harman, Troch, Brooks, & Sivapalan, 2011), the presence of forest vegetation may mediate sensitivities to interannual snowpack variability. In contrast, meadows occurring in more barren watersheds with less subsurface storage are, perhaps, more reliant on localized sources of snowmelt runoff and infiltration and are, thus, more sensitive. Other watershed-scale variables that suggest high watershed subsurface storage capacity and recharge—meadows in more convex basins (Figure 7i), with higher values of soil available water storage capacity (Figure 7d); extrusive igneous geologic types (Figure 7f); and larger proportions of their watersheds composed of low slope and valley landforms (Figure 7j) that promote lateral flow—also exhibit lower climate sensitivities, but effect sizes of these drivers were smaller (Table 3). The fact that the watershed forestedness variable was a better predictor of sensitivity than other watershed surface or subsurface attributes may in part be due to the fact that vegetation cover is more completely and accurately observed relative to the other subsurface and climate variables we used. Other recent studies have similarly suggested that vegetation patterns can provide useful insights into below-ground processes related to hydrologic partitioning (Hwang, Band, Vose, & Tague, 2012; Thompson et al., 2011).

Long-term average meadow greenness was the third strongest predictor of sensitivity, with sensitivity peaking at intermediate (0.45–0.6) values of NDVI (Table 3 and Figure 7h). Sensitivity was consistently higher at these intermediate values regardless of meadow climate or watershed forestedness (Figure 8). This metric was included to provide an overall indication of site productivity and, to a limited extent, vegetation composition. High values (>0.6) typically indicate dense and/or forested vegetation cover, intermediate values (0.2–0.6) indicate herbaceous or shrub cover, and low values (<0.2) indicate barren vegetation types (Jensen, 2007). Given that this metric is based on an average across the entire meadow site, the interpretation of intermediate values as an indication of composition is not straightforward because they could result from a wide range of vegetation compositions. Despite this uncertainty, these results suggest that meadow sensitivity tends to be lower in more barren and more densely vegetated meadows than in meadows with more mixed vegetation composition and intermediate levels of biomass production. This pattern could potentially represent a gradient of water availability from xeric to mesic to hydric. Intermediate values also may be an indicator of mesic meadow types, which have been shown in other regions to exhibit higher sensitivities to climate variability relative to more xeric or hydric meadows (Debinski, Jakubauskas, & Kindscher, 2000; Debinski, Caruthers, Cook, Crowley, & Wickham, 2013; Debinski, Wickham, Kindscher, Caruthers, & Germino, 2010).

Other meadow-scale variables such as size, shape, and soil available water storage explained smaller amounts of variation in sensitivity among meadows (Table 3 and Figure 7e,g). These results suggest that large meadows with small perimeter to area ratios are less sensitive to climate variability. The direction of the response is consistent with hypothesized responses, given that these meadows are likely to be less susceptible to encroachment by upland species and have greater capacity for water storage and buffering of high flow events (Viers et al., 2013). However, sensitivity estimates for small meadows with large perimeter to area ratios may be more influenced by meadow-adjacent vegetation than larger meadows, which may have contributed to this result.

Meadows (and watersheds) with more soil available water capacity (Table 3 and Figure 7d,e) were less sensitive to snowpack variability, which is also consistent with hypothesized responses. Available water capacity increases with increasing soil depth, which can serve to enhance connectivity with the water table and decreasing particle size, which serves to store and hold more water later into the season (Lowry & Loheide, 2010). This result suggests that despite the limitations of the USDA SSURGO data (i.e., maximum soil depth is only 201 cm, relatively coarse mapping), these may still have some utility in deciphering differences in meadow and/or watershed responses to climate variability at a landscape scale.

Given the recent drought and associated tree mortality in the Sierra Nevada (Tree Mortality Task Force, 2018), contemporary studies have addressed the impacts of tree density reductions due to forest thinning or fire on ET and surface water availability (Boisramé, Thompson, Collins, & Stephens, 2017; Roche, Goulden, & Bales, 2018). We included fire return interval departure—an indicator of tree density relative to historic conditions and associated fuels loading and ET—to assess how meadow sensitivity varies among departure classes. Although this classification helped to explain some variance in our model (as indicated by variable importance; Table 3), the effect sizes were very small and, in most cases, not statistically significant. Sensitivity of meadows in watersheds with the majority of vegetation classified as departed due to decreased fire frequency (suggesting increased tree densities) relative to historical conditions was not detectably different from those in watersheds in which fire frequency is consistent with historic regimes. It is possible that any signal in these data may simply be overwhelmed by the strong environmental gradients that exist across the study area, as fire effects may differentially affect watershed-scale ET rates across gradients of water availability (Roche et al., 2018). Moreover, fire return interval departures do not explicitly account for fire severity and thus may not necessarily be indicative of ET water use.

The human modification variable included in our analysis also captures large areas where substantial forest cover changes occurred due to tree clearing (i.e., from timber harvest), as determined by changes in vegetation classification from forest to grassland between time steps in the National Land Cover Database in places that were not burned (Theobald et al., 2016). Although this variable captures other types of human modification related to urban, energy, and transportation infrastructure, most of the areas in the Sierra Nevada exhibiting human modification are associated with tree clearing (https://disappearingwest.org/map/). Our results indicate moderate decreases in sensitivity with increasing human modification (Figure 7c), which, if this is a signal of increased water availability in more heavily logged watersheds, would be consistent with the hypothesis that reduced tree cover at the watershed scale increases water availability to meadows. However, other studies have suggested that heavily logged or burned basins exhibited accelerated snowmelt and earlier runoff, which might confer higher sensitivity (Coats, 2010; Stevens, 2017). Given the complex hydrological interactions between forest cover, climate, and watershed processes, and wide variation in these conditions across our study area, the interpretation of this result is not straightforward and any causal relations between loss of woody vegetation and meadow sensitivity will require a more tightly controlled and smaller scale study. Similarly, connecting other types of human modifications represented in this dataset with meadow sensitivities will require more tightly controlled studies to tease apart additional and potentially opposing human influences such as roads, grazing, and human development.

One of the objectives of our study was to evaluate how well existing spatial datasets capture variation in HGM controls on meadow sensitivity to climate. Our dataset consisted of a large sample size of meadows across a highly heterogeneous landscape and our analysis explained just under 50% of the variation in sensitivities of late-season water availability to snowpack among meadows, suggesting substantial unexplained variability. This unexplained variability is, in part, driven by unmeasured local-scale factors related to groundwater flow patterns, variations in soils and vegetation, disturbance history, and localized elevational gradients. However, unexplained variance could also be due to poorly measured variables, which are inherent in coarse scale datasets, particularly those related to soils, geology, and climate that are interpolated from sparse observations. Despite this, robust patterns in vegetation sensitivities to snowpack were observed in relation to (a) average climate (dry to wet), (b) dominant watershed land cover (forested to barren), and (c) indicators of meadow vegetation productivity and composition (long-term average meadow greenness), in particular. Although meadow sensitivity responses to variables related to topography and subsurface characteristics (geology, soils) were consistent with our hypotheses in terms of the direction of the response, the magnitudes were generally weaker, suggesting more limited predictive value of these datasets at the Sierra-wide scale relative to the former three variables.

Numerous studies have examined climate sensitivities of streamflow in the Sierra Nevada (e.g., Maurer, Stewart, Bonfils, Duffy, & Cayan, 2007; Stewart, Cayan, & Dettinger, 2005; Young et al., 2009), but few have attempted to link these sensitivities to a large suite of physical characteristics beyond elevation, latitude–longitude, and aspect (Stewart, 2013). Stewart (2013) examined climate sensitivity of streamflow to watershed physical characteristics in the Sierra Nevada and found that high-elevation, snowmelt-dominated basins on the western Sierra Nevada slopes have historically exhibited the greatest sensitivity to climate change. This paper also suggested that watersheds with lower proportions of basaltic rock geologies and low percentages of forested land cover tended to be more sensitive but that these effects could not readily be teased apart from elevation due to the covariance of many of these variables. Although results from our analysis are generally consistent with this study, our analytical approach, which extracts latent variables that are orthogonal (uncorrelated), avoids this issue of covariance, providing greater clarity about the physical patterns that relate to sensitivity. Moreover, our approach allowed us to quantify the independent contributions of physical site and watershed characteristics relative to each other over a much larger number of sites than has previously been accomplished using streamflow records.

An important caveat is that our analysis may have missed some of the most vulnerable meadows, as (>10,000) meadows that did not reach our minimum size threshold and meadows that have already disappeared due to land cover or climatic changes were not included. Also, this analysis was based on climate sensitivity of meadow vegetation occurring within contemporary meadow footprints, so does not explicitly account for meadows that have changed size over the course of the 31-year study period, a pattern that is well-documented in this region and is attributable to conifer encroachment (Lubetkin, Westerling, & Kueppers, 2017). Finally, the climate sensitivity metrics used in this analysis characterize one aspect of climate sensitivity of vegetation relating to late-season water availability. Meadow vegetation that exhibited low climate sensitivity in this study may still be sensitive to climate variability and change in other ways relating to, for example, other aspects of phenology, species composition, or biomass production, or because they are sensitive to longer varying climatic changes, as opposed to interannual variability, as was studied here. The data and methods developed as part of this study are well suited to assess these alternate forms of climate sensitivity in the future.

5 | CONCLUSIONS

In this study, we demonstrate a transferrable approach for understanding and monitoring responses of meadow ecosystems to climate variability using remote-sensing-based indicators and a water balance model. Platforms such as Google Earth Engine (Gorelick et al., 2017) and cloud-computing applications such as Climate Engine (http://climateengine.org/; Huntington et al., 2017) have provided free access to—and highly efficient processing of—climate and remotely sensed information that can be used to quantify ecological sensitivities to climate and monitor other drivers of change ranging from site specific (e.g., Hausner et al., 2018) to regional (as demonstrated in this study) scales.

We found that late-season vegetation conditions in most meadows were more sensitive to snowpack than to precipitation or evaporative water demand. We also found that sensitivities covaried considerably across the study extent, with long-term meadow climate, watershed forestedness and other characteristics indicative of subsurface water storage capacity, and with indicators of meadow vegetation composition and biomass. Overall, subalpine and alpine meadows—those that have high average snowpack/precipitation amounts but low subsurface storage capacity—exhibited the largest sensitivities to annual snowpack in our study. Numerous studies on fine-scale hydrologic processes related to meadow structure and function in the Sierra Nevada exist, but to our knowledge, this is the first study to address meadow sensitivities to snowpack at a regional scale. Given that similar climatic patterns and hydrological processes dictate meadow structure and function in montane systems across the western United States where the majority of precipitation occurs as snow during the winter season, the climate, watershed, and meadow-scale drivers we identified could similarly influence variability in meadow climate sensitivities in these regions.

Our results may be useful for considering and prioritizing the siting of meadow conservation or restoration efforts, given the clearly important role of landscape context in mediating climate sensitivities of meadows. They further complement existing datasets characterizing other aspects of meadow adaptive capacity (e.g., Maher et al., 2017). Moreover, the datasets developed as part of this project can provide valuable information to practitioners to better understand the broader landscape context of a given meadow, how it compares to the larger population of meadows in the region, and how it may respond to changing climate. For example, alpine and subalpine meadows occurring in basins with little subsurface storage capacity are likely to be more immediately vulnerable to changes in rain: snow partitioning and earlier snowmelt associated with climate warming than meadows in watersheds with deeper soils and more storage. In these places, it will be particularly important for managers to consider management objectives that are robust to a range of potential future conditions and that account for the impacts of climate on project success (Stein, Glick, Edelson, & Staut, 2014). Our results further highlight the major environmental gradients along which meadow sensitivities vary, providing a useful framework for isolating the influences of management actions from those caused by natural variability.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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