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Feeding the fire: Annual grass invasion facilitates modeled fire spread across Inland Northwest forest-mosaic landscapes

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Abstract

Invasive annual grasses are a growing global concern because they facilitate larger and more frequent fires in historically fuel-limited ecosystems. Forests of the western United States have remained relatively resistant to invasion by annual grasses and their subsequent impacts. However, where forests are adjacent to invaded areas, increased fire spread across ecotones could alter fire behavior and ecosystem resilience. In the Inland Northwest, USA, recent invasion by the annual grass *ventenata* (*Ventenata dubia*) has increased fine fuel loads and continuity in nonforest patches embedded within the forested landscape. Despite *ventenata*'s rapid spread across the American West and growing management concern, little is known regarding how invasion influences fire within invaded vegetation types or its potential to alter landscape-scale fire and management practices. Here, we examine how the *ventenata* invasion alters simulated fire across forest-mosaic landscapes of the 7 million ha Blue Mountains Ecoregion using the large fire simulator (FSim) with custom fuel landscapes: present-day invaded versus historic uninvaded. Invasion increased simulated mean fire size, burn probability, and flame lengths throughout the ecoregion, and the strength of these impacts varied by location and scale. Changes at the ecoregion scale were relatively modest given that fine fuels increased in only 2.8% of the ecoregion where *ventenata* invaded historically fuel-limited vegetation types. However, strong localized changes were simulated within invaded patches (primarily dwarf-shrublands) and where invasion facilitated fire spread into nearby forests. Within invaded patches, burn probabilities increased by 45%, and higher flame lengths required fire management strategies to shift from direct to indirect attack, requiring large machinery. Forests with 25% of their neighborhood invaded experienced a 28% increase in burn probability and 16% increase in the probability of experiencing flame lengths likely to

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produce crown fire (flame lengths >2.4 m). Increased canopy loss could have severe implications for forest resilience given that invasive grasses can heavily invade early seral dry conifer forests and limit postfire forest recovery. Our study demonstrates how annual grass invasion can influence fire behavior and resilience across forest landscapes despite primarily invading nonforested areas, and highlights invasion as an important management issue in an expansive forest-mosaic ecosystem.

KEYWORDS

FSim, fuels, grass-fire cycle, ventenata, wildfire, wildfire modeling

INTRODUCTION

Invasive grasses are a growing global concern because they increase fine fuels and facilitate larger and more frequent fires in previously fuel- or fire-limited desert, shrub-steppe, and savannah ecosystems (Brooks et al., 2004; D'Antonio & Vitousek, 1992; Kerns et al., 2020). In these historically fire-resistant ecosystems, changes in fuels and fire regimes, including more frequent, uncharacteristic, or severe fire, often result in the loss of fire-sensitive native vegetation and altered ecosystem function (D'Antonio & Vitousek, 1992; Hessburg et al., 2005). Ecosystems that evolved with low to moderate severity and frequent fire, including many forests of the western United States, have been relatively resistant to grass invasion (Martin et al., 2009; Rejmánek et al., 2013) and subsequent positive grass-fire feedbacks, commonly known as “grass-fire cycles” (D'Antonio & Vitousek, 1992). However, forests could become susceptible to invasion impacts if fires in invaded areas increased spread into and between adjacent forests, potentially altering landscape-scale fire regimes and postfire tree regeneration (Kerns et al., 2020). While grass-fire cycles are well documented in many shrub-steppe and desert ecosystems (Brooks et al., 2004, 2016; D'Antonio & Vitousek, 1992; Keeley, 2000), there remains a gap in knowledge about how these species influence fire and ecosystem function in forest-mosaic landscapes composed of forest and nonforest patches (Fusco et al., 2019). This information is critical for designing and implementing effective fuel and fire management strategies for grassy and woody fuels to promote landscape resistance and resilience.

The spatial arrangement of vegetation and fuels influences landscape-scale fire patterns and behavior. Landscapes with high heterogeneity (e.g., forest mosaics) are generally considered to have slower fire spread rates and greater overall fire resistance than landscapes of homogeneous forest, given that nonforest portions of the mosaic are likely to have lower fuel loads and/or flammability and

may act as natural fire breaks (Collins & Stephens, 2007; Duguy et al., 2007; Hessburg et al., 2005; Parks et al., 2015). The homogenization of forests and increased fuel loads as a result of fire suppression and forest encroachment into nonforest patches have been associated with more severe fires and increased landscape-scale fire spread, in part due to more difficult containment (Hessburg et al., 2005). In these areas, fuel reduction and fuel break treatments are common tools utilized to reduce fire hazard by fragmenting areas of continuous fuel and reducing overall fuel loads to slow fire spread and reduce flame lengths (Finney, 2001). Invasion of flammable grass into nonforest patches could contribute similarly to landscape homogenization by increasing fuel loads and connectivity, acting as fuel “conveyor belts” for surface fire across the landscape (Hessburg et al., 2005; Kerns et al., 2020). While there has been much focus on the use of woody fuel treatments to mitigate wildfire size and severity and promote ecosystem resistance (Agee & Skinner, 2005; Prichard et al., 2020; Prichard & Kennedy, 2014; Wei, 2012), there has been little examination of how the spatial arrangement of invasion influences fire behavior in dry forests and forest-grass mosaics or how treating grass invasions may help meet fire-related management goals.

Positioned at the center of a recent annual grass invasion, the Blue Mountains Ecoregion (BME) of the Inland Northwest, USA, presents an opportune place to investigate the impacts of grass invasion on fire in a forest-mosaic landscape. The landscapes that make up the BME are highly heterogeneous and comprise a patchwork of forest interspersed with sparsely vegetated low productivity dry meadows and dwarf-shrublands locally known as “forest scablands.” These meadows and scablands do not support forests and are maintained by extremely shallow soils rather than frequent low-severity fire. Until recently, these areas were resistant to widespread grass invasion (Johnson & Swanson, 2005). However, a recently introduced invasive annual grass, ventenata (*Ventenata dubia*), has heavily invaded many forest scablands (Tortorelli et al., 2020),

where it increases fuel loading and continuity in previously fuel-limited patches within the forested mosaic (Gibson, 2021). Ventenata also invades dry, open pine forests throughout the region and is often abundant in severely burned forests adjacent to scablands following canopy loss (Downing et al., 2020; Tortorelli et al., 2020). Ventenata grows in dense patches and has a high surface-area-to-volume ratio resulting in a quick-drying fuel that senesces earlier in the fire season than many native perennial species (personal observation, unpublished data), much like the invasive annual grass cheatgrass (*Bromus tectorum*; Brooks et al., 2004; Davies & Nafus, 2013). As with cheatgrass across much of the American Great Basin (Brooks et al., 2004; Davies & Nafus, 2013), the potential for ventenata to alter fuels and fire behavior is substantial, which contributes to its high management concern throughout the BME (Hallmark & Romero, 2015). Despite these concerns, the direct effects of the ventenata invasion on fire behavior within invaded areas and transmission across surrounding landscapes have yet to be measured.

In this study, we use a novel application of the large fire simulator (FSim; Finney et al., 2011) to model the effects of annual grass invasion on fire spread, burn probability (BP), and flame lengths throughout the 7 million ha BME. A simulation-based study allows for extensive exploration of the effect of invasion on landscape-scale fire while holding all other factors (e.g., fire weather and ignitions) constant. We developed specific spatial fuel layers that captured the landscape (1) prior to invasion and (2) presently with the invasion that provided information for two simulations (“uninvaded” and “invaded”). We then evaluated how the model output differed at local to landscape scales and within different vegetation types for the two simulations. Our aims were to characterize how ventenata and the spatial patterns of invasion alter simulated fire spread, BP, and flame lengths at multiple spatial scales, including individual forest cells, continuous invaded patches, landscapes (~100 ha), and the entire ecoregion.

Invasion into historically sparsely vegetated forest openings (nonforest patches) and ecotones may impact fire resistance through multiple mechanisms and at different spatial scales, and this may have important implications for forest resilience. We predicted that invasion would dramatically increase ignitability and flame lengths in nonforest patches and facilitate fire spread across forest ecotones and into adjacent forests (Figure 1). We expected the magnitude of fire impacts to vary depending on the extent of the invasion within the larger forested mosaic, with greater shifts in BP and fire behavior in larger invaded patches, and in forested areas and landscapes with a high proportion of invasion in their immediate neighborhood.

MATERIALS AND METHODS

Study area

The study area is the 7 million ha BME, as defined in the EPA Ecoregion Level III (Figure 2; Omernik & Griffith, 2014). The climate regime is temperate with precipitation and temperatures varying along topographic and elevational gradients. On average, the region receives between 27 and 57 cm of precipitation each year, primarily falling between November and June. High temperatures average in the upper 20s °C and lows in the −10s °C (PRISM Climate Group, 2019). Vegetation across the ecoregion is a highly variable mosaic of forest and nonforest vegetation types (Figure 2). Closed and open canopy forests are primarily composed of Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) with increasing grand fir (*Abies grandis*) and western larch (*Larix occidentalis*) at higher elevations and western juniper (*Juniperus occidentalis*) woodlands at lower elevations. Forested areas are commonly interspersed with lithic scabland soils on plateau uplands supporting sparsely vegetated dwarf-shrublands composed of scattered shallow-rooted bunchgrasses and, in many cases, low-growing sagebrush species, such as stiff sagebrush (*Artemisia rigida*) and low sagebrush (*Artemisia arbuscula*; Figure 2; Johnson & Swanson, 2005). More productive nonforest vegetation types include perennial bunchgrass grasslands in the northeast corner of the ecoregion and big sagebrush steppe concentrated in the west and southeast sections of the ecoregion (Figure 2). Closed and open canopy forests are the most prevalent vegetation types across the study area (collectively 51%), followed by dry shrubland, primarily big sagebrush steppe (24%), herbaceous grassland (9%), dwarf-shrubland (7%), agriculture (3%), recently disturbed (2%), nonvegetated (2%), sparsely vegetated (1%), and wetland and riparian (1%) (Figure 2; Appendix S1; LANDFIRE, 2019a).

Fuel characterization: Creating custom landscapes

To address our aims, we required two data layers representing landscape fuels (“fuelscapes”) for our simulations (“uninvaded” and “invaded”) that best represented the nonforest fuels associated with the study area without and with ventenata, respectively. We created the two custom fuelscapes based on modifications to the Landscape Fire and Resource Management Planning Tools (LANDFIRE) 2.0.0 fuel model grid (LANDFIRE, 2019b) as described below. This version of LANDFIRE represents vegetation

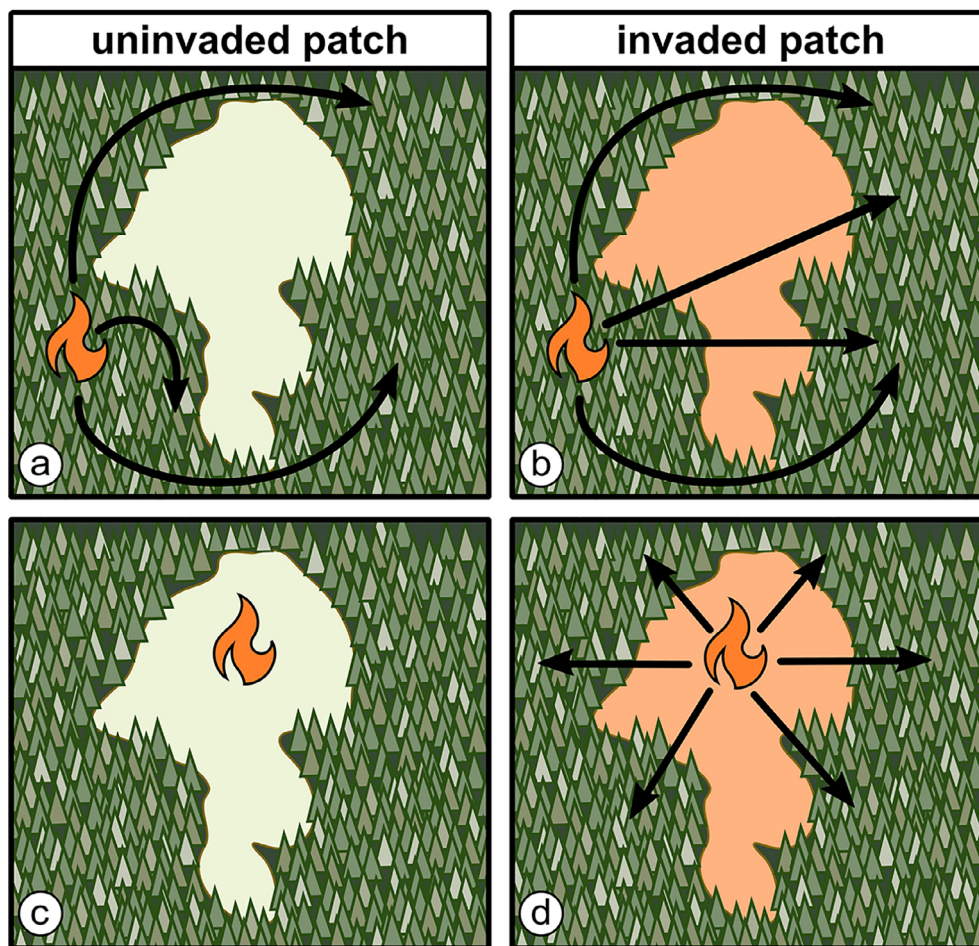


FIGURE 1 Predicted differences in the spatial arrangement of vegetation and fuels associated with grass invasion can influence landscape-scale fire patterns and behavior. (a, b) Differences in fire spread when a fire is ignited in the forest and travels either (a) around the uninvaded nonforest patch or (b) across the invaded nonforest patch into the adjacent forest. (c, d) Fire behavior differences when a fire is ignited within the patch. (c) Fire fails to spread into the surrounding forest because the uninvaded patch lacks a continuous fuel bed. (d) Fire readily spreads across the invaded patch and into the surrounding forest.

conditions for the end of 2016. It is customary to modify the LANDFIRE fuel model grids based on the availability of specific and improved local data and sources (Scott et al., 2012, 2016; Thompson et al., 2012). However, to our knowledge, specific modifications owing to grass invasion have never been attempted; therefore, we detail our novel fuelscape development below.

The uninvaded fuelscape was created in two stages. First, we developed a core ventenata habitat layer to depict areas with historically low fuel loads where we expected the ventenata invasion to have the greatest impact on fuel load and structure. We selected vegetation types that (1) were historically relatively fire resistant with fine fuel loads less than 897 kg ha^{-1} ; (2) are generally not heavily impacted by other annual grass invasions, including cheat-grass; and (3) are at high risk for ventenata invasion given their vegetation associations (Jones et al., 2018; Nietupski, 2021; Tortorelli et al., 2020). Vegetation types

included in the vegetation layer were determined through discussions with ecologists, botanists, and weed managers. All core habitat types were combined into a single 120-m resolution raster in ArcGIS for the study area and a 30-km buffer, which is consistent with FSim model inputs. The core habitat layer covered 959,721 ha, 13.5% of the study region (Figure 3). See Appendix S2 for additional details, including a complete list of vegetation types included.

LANDFIRE fuel models (Scott & Burgan, 2005) appeared to overestimate fuel loads and spread rates in many places within the core habitat layer. Therefore, we reassigned these areas to fuel models that more accurately reflected lower fuel loads prior to invasion based on our field observations, expert opinion, and herbage estimates (Gibson, 2021; Johnson & Swanson, 2005). Areas classified as fuel models GR2 (Low Load, Dry Climate Grass) were reclassified as GR1 (Short, Sparse Dry Climate Grass) and

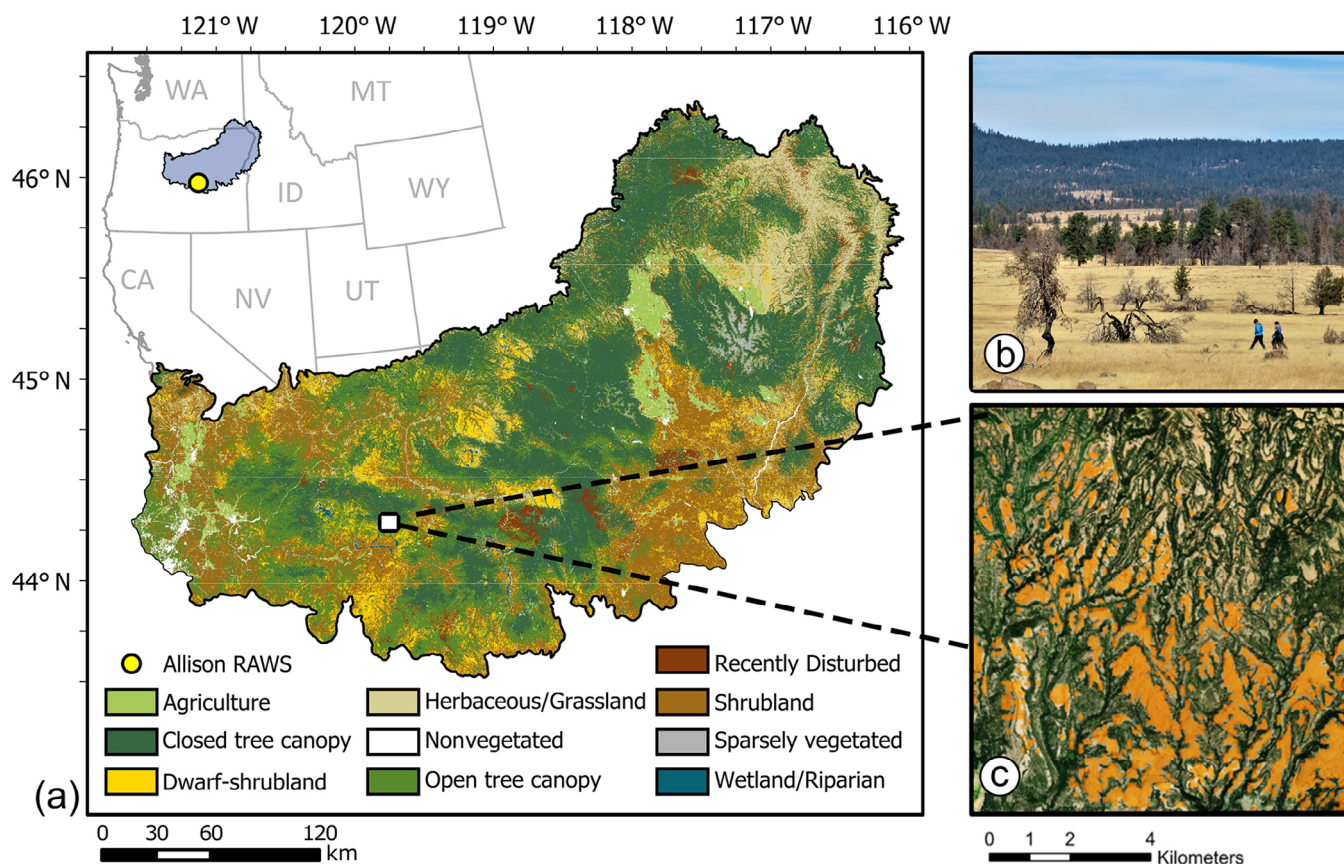


FIGURE 2 (a) Blue Mountains Ecoregion mapped by vegetation type (modified from LANDFIRE 2.0.0 Existing Vegetation Type; Appendix S1) and location of Remote Automated Weather Station (RAWS) used for FSim calibration. (b) Depiction of a forest-mosaic landscape following the 2015 Corner Creek fire, where fire spread through invaded dwarf-shrublands into forested islands and the surrounding forest matrix. (c) Aerial imagery displaying the forest-mosaic landscape with invaded areas shaded orange (Nietupski, 2021).

areas classified as GS2 (Moderate Load, Dry Climate Grass-Shrub) were reclassified as GS1 (Low Load, Dry Climate Grass-Shrub; Appendix S3). The spatial arrangement of these fuels then served as our uninvaded fuelscape for analysis.

To create the invaded fuelscape, we reassigned fuel models from the uninvaded fuelscape to reflect higher fuel loads where *ventenata* had invaded within our core habitat layer (Figure 3). Invaded areas were determined using a newly developed *ventenata* distribution map for the BME (Nietupski, 2021). This map identified *ventenata* presence greater than 20% cover as estimated from land surface phenology, climate, and biophysical indicators derived from remotely sensed data. *Ventenata* invaded 7.7% of the ecoregion according to these estimates; however, we only reassigned fuel models in 2.8% of the study region (190,565 ha) where invasion overlapped low-productivity vegetation types represented in the core habitat layer (Appendix S3). Fuel models were reassigned to represent increased fine fuel loading and spread rates in invaded areas, and where shrubs were present, a shift from woody to fine fuel-driven fire behavior (Table 1; Scott & Burgan, 2005), based on our field observations, discussions with experts,

and biomass estimates from invaded dwarf-shrublands (Gibson, 2021). LANDFIRE vegetation types in invaded core habitat areas were classified as 58% dwarf-shrubland, 20% shrubland, 11% herbaceous/grassland, and 10% open tree canopy. The remaining 1% was spread among the remaining vegetation types identified above.

Wildfire simulation modeling: The FSim

We used FSim (Finney et al., 2011) to simulate wildfire throughout the study area. FSim is a spatially explicit model that uses a set of Monte Carlo style simulations to predict ignitions, fire spread, and containment across the landscape over thousands of yearly weather sequences, resulting in maps of BP and flame length probability (Finney et al., 2011). FSim is described in detail elsewhere (Finney et al., 2011), as are its applications to a diversity of spatial fuel management, planning, and risk analysis studies. FSim steps through each day in a fire season, where fire weather conditions are generated from daily weather records gathered from a nearby, representative weather station to represent realistic weather

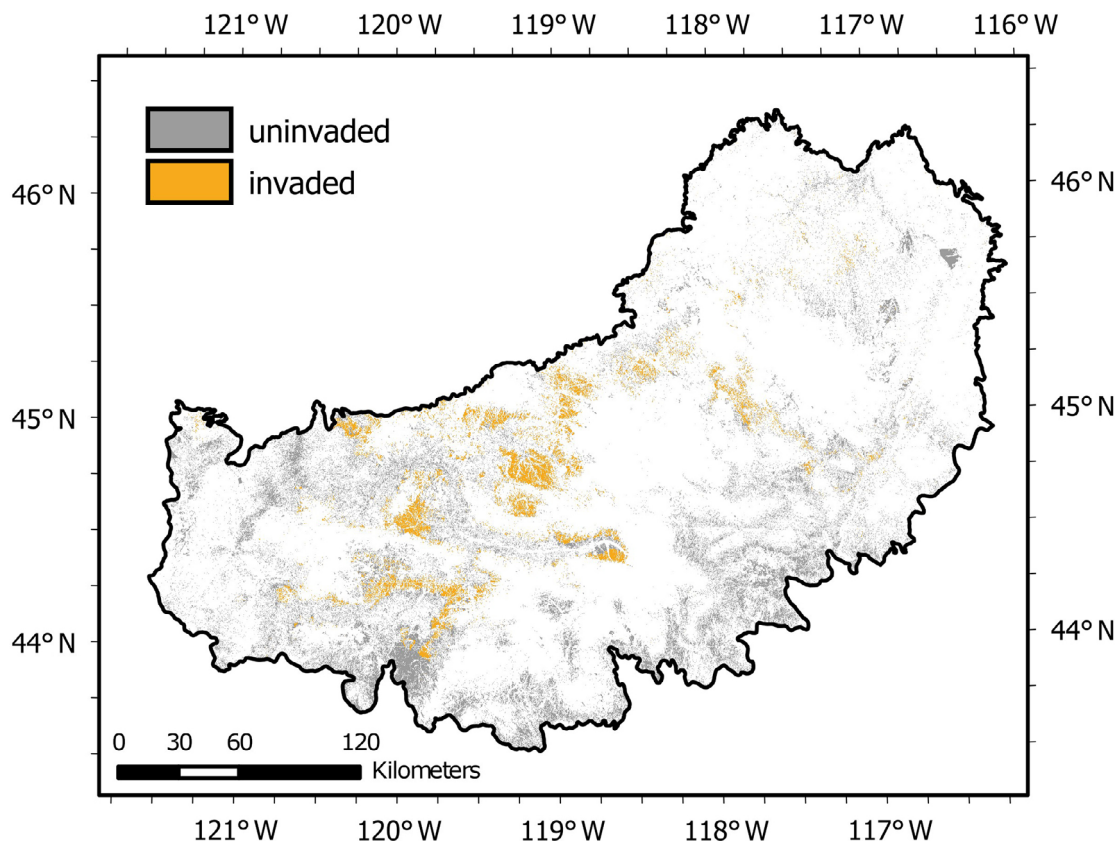


FIGURE 3 The sparsely vegetated core habitat layer displaying areas where fuel models were reassigned to represent invasion in the invaded simulation according to the ventenata invasion map (Nietupski, 2021) and core habitat that remained uninvaded in the invaded simulation.

TABLE 1 Fuel models (Scott & Burgan, 2005) were reclassified to represent increased fine fuel loading and fire spread rates in invaded areas within the core habitat layer, as represented below (e.g., areas classified as GR1 in the uninvaded fuelscape were reclassified as GR2 when invaded).

Uninvaded fuelscape		Invaded fuelscape	
Model abbreviation	Model description	Model abbreviation	Model description
NB9	Bare ground →	GR2	Low Load, Dry Climate Grass
GR1	Short, Sparse Dry Climate Grass →	GR2	Low Load, Dry Climate Grass
GS1	Low Load, Dry Climate Grass-Shrub →	GS2	Moderate Load, Dry Climate Grass-Shrub
SH2	Moderate Load, Dry Climate Shrub →	GS2	Moderate Load, Dry Climate Grass-Shrub
SH1	Low Load, Dry Climate Shrub →	GS2	Moderate Load, Dry Climate Grass-Shrub
TL3	Moderate Load Conifer Litter →	TU1	Low Load, Dry Climate Timber-Grass-Shrub

sequences for the simulation period (Grenfell et al., 2010). On each simulated day, FSim stochastically determines ignitions based on relationships between historical energy release component (ERC) and large fire ignitions for the study area (Cohen & Deeming, 1986) and an ignition probability grid built from historical fire occurrence data (Andrews et al., 2003). After ignition, fire spread is simulated using wind speed and direction, ERC, landscape topography, and fuel characteristics following a minimum travel time (MTT) algorithm

(Finney, 2002; Rothermel, 1972). Suppression is simulated using an algorithm that determines the probability of daily containment based on vegetation type, time since ignition, and fire behavior (Finney et al., 2009).

FSim outputs include (1) raster grids of annual BP; (2) the conditional probability of a pixel burning within six flame length classes, given that a fire occurs (CBP_i); (3) a fire size list including the locations of ignitions for each simulated fire; and (4) shapefiles of all simulated fire perimeters. The BP for a given pixel is calculated as

the number of times a pixel burns divided by the number of years in the simulation (here, 10,000). CBP_i are calculated from fireline intensity and take into account information about fuel moisture, wind, the direction from which fire encounters each pixel, (i.e., as heading, flanking, or backing fire), and their slope and aspect (Finney, 2002). The six flame length classes are 0–0.6, >0.6–1.2, >1.2–1.8, >1.8–2.4, >2.4–3.7, and >3.7 m. The sum of CBP_i adds up to 1 for each pixel or 0 if the pixel never burned (e.g., in nonburnable areas).

We first ran FSim using the invaded fuelscape at 120-m resolution. We calibrated FSim to approximate the distribution of size and frequency of fires larger than 100 ha recorded in the USFS Fire Occurrence Database (FOD) from 2000 to 2017 (Short, 2021), assuming these years reasonably represent the recent invasion footprint. Weather data were obtained from the Allison remote automated weather station (RAWS, 43.92° N, –119.59° E), located within the study area (Figure 2). Topography (slope, aspect, and elevation) and canopy data (canopy bulk density, base height, cover, and height) were extracted from LANDFIRE (LANDFIRE, 2016), and aggregated from 30- to 120-m resolution using nearest neighbor resampling in ArcMap 10.8.1. We ran the simulation for 10,000 years to ensure that each pixel in the landscape had an opportunity to burn numerous times, and we adjusted parameters so that mean fire size and number of fires fell within the 70% confidence intervals around observed values (Appendix S4; Scott et al., 2018). Average annual BP simulated by FSim was 0.0083, similar to the observed value (0.0087). After FSim was calibrated using the invaded fuelscape, we simulated uninvaded conditions by replacing the invaded fuelscape with the uninvaded fuelscape, holding all other model inputs and parameters, including modeled ignition timing and locations and weather conditions, constant. Holding all model inputs and parameters constant allows us to compare the two simulations to capture the differences caused by the fuelscapes, as described below.

Data analysis

Burn metrics: Ecoregion scale

To represent a meaningful shift in flame lengths between the uninvaded and invaded simulations for estimating ecosystem effects and interpreting management outcomes, we calculated the conditional probability of each pixel burning at moderate and high flame lengths: flame lengths exceeding 1.2 m ($CBP_{>1.2m}$) and 2.4 m ($CBP_{>2.4m}$). We chose these thresholds because flame lengths above 1.2 m often require a shift in fire management and

suppression practices from direct attack with hand tools to indirect attack using large machinery or aerial retardant (Andrews & Rothermel, 1982) and can lead to increases in crown fire (Ager et al., 2014; NWCG, 2006). Flame lengths exceeding 2.4 m often result in crown fire and can lead to tree mortality in dry mixed conifer forests depending on diameter and canopy base height (Ager et al., 2010, 2014). We also calculated the proportion of the study area that is likely to burn at moderate and high flame lengths (conditional on burning) for the uninvaded and invaded simulations by multiplying the study area (in hectares) by $CBP_{>1.2m}$ and $CBP_{>2.4m}$. We primarily focused our analyses on shifts in $CBP_{>1.2m}$ when summarizing ventenata effects on fire behavior in nonforested areas (e.g., dwarf-shrublands), as these vegetation types lack tree canopies to carry fire.

To examine how invasion may influence burn metrics at the ecoregion scale, we compared the mean number of large fires (>100 ha), fire size, BP, $CBP_{>1.2m}$, $CBP_{>2.4m}$, and area burned at moderate and high flame lengths between the uninvaded and invaded simulations for the entire ecoregion. We also calculated mean and median BP and $CBP_{>1.2m}$ by vegetation type and for invasion-adjacent areas (3-km buffer around invaded patches and excluding invaded areas) and compared these between the two simulations. Absolute differences between invaded and uninvaded simulations (invaded – uninvaded) and proportional differences (absolute difference/uninvaded) were calculated for each vegetation type, for all areas where fuels were adjusted to represent invasion (“invaded core habitat”), and for the entire study area.

Fire transmission

To assess how ventenata invasion may influence large fire spread across the forest mosaic, we compared fire transmission patterns in the invaded and uninvaded simulations. For each simulated fire perimeter, we recorded the vegetation type of the ignition cell and the area burned for each vegetation type within that fire perimeter using the ArcGIS toolbox XFire (Kingbird Software, 2018). From these data, we summarized mean area burned per year for each burned vegetation type by ignition vegetation type for both simulations. To focus analysis on large fires that were more likely to have spread and cross between vegetation types, we subset the data to include only fire perimeters from the uninvaded simulation that were >100 ha. We included fires from the invaded simulation with corresponding ignitions. Fire perimeters that ignited outside of the study area (in the 30-km buffer) were removed prior to this analysis. In total, we analyzed 209,078 fire perimeters from each simulation.

Spatial patterns of fire: Local forest, patch, and landscape scales

We modeled the influence of invasion patterns on burn metrics at various scales, including forest cells, patches of continuous invaded core habitat, and averaged across ~100 ha landscapes using generalized additive models (GAMs; Hastie & Tibshirani, 1987). All GAMs were fit with a binomial family from the R package “gam” (Hastie, 2022).

We examined the effect of invasion on fire behavior in uninvaded forest cells by relating forest burn metrics to the proportion of invaded area within the surrounding neighborhood. Areas adjacent to invaded patches are the most likely to show changes in fire behavior, and neighborhood analyses complement an ecoregion-wide assessment. The focal forest cells were classified as the cell at the center of each 116.6 ha (1080 m × 1080 m, or 9 × 9 cells) neighborhood determined using a moving window. Only cells classified as uninvaded and forest (open or closed canopy) were included as focal forest cells. A neighborhood size of 116.6 ha was chosen to approximate the 100 ha fire size considered by FSim to constitute the threshold for a “large fire.” We developed separate GAMs to examine how BP, $CBP_{>1.2m}$, and $CBP_{>2.4m}$ in forested cells were influenced by proportion of invasion (and corresponding uninvaded core habitat for the uninvaded simulation) in the surrounding neighborhood. We also fit models to demonstrate how BP and CBP differed when the corresponding core habitat areas were uninvaded. To narrow the sample size and focus the analysis on the effect of varying levels of landscape invasion, we only included cells that had some level of invasion in the surrounding neighborhood, resulting in a sample size of 357,182 focal forest cells and corresponding neighborhoods. Neighborhood calculations were performed using the “focal” function from the R package “raster” (Hijmans, 2020).

To investigate how the size of an invaded patch influenced within-patch fire behavior, we first identified patches as continuous areas of invaded core habitat with

connections in any of eight directions. Patch size was measured as the sum of core habitat area that made up each patch using the “extract_lsm” from the package “landscapemetrics” (Hesselbarth et al., 2019). Then we calculated the average BP and $CBP_{>1.2m}$ for each invaded patch ($n = 17,783$) in the invaded simulation and the same fire metrics for the corresponding core habitat areas when uninvaded for the uninvaded simulation. Finally, we modeled the response of within-patch BP and $CBP_{>1.2m}$ to patch size (log hectares) using separate GAMs.

To examine how invasion influenced landscape-scale BP and fire behavior across heterogeneous forest-mosaic landscapes and to identify potential invasion thresholds for influencing landscape-scale fire, we related landscape BP, $CBP_{>1.2m}$, and $CBP_{>2.4m}$ for the invaded and uninvaded simulations to the proportion of invaded area within the 116.6 ha neighborhoods defined above. Landscape burn metrics were calculated as the average of each burn metric across the entire landscape using a moving window analysis from the package “raster” (Hijmans, 2020). We developed separate GAMs to examine how the proportion of the invaded landscape (and corresponding uninvaded core habitat) influenced landscape BP, $CBP_{>1.2m}$, and $CBP_{>2.4m}$. We included only landscapes where the proportion invaded was greater than zero, as described above. In total, 789,062 individual landscapes were analyzed. All spatial pattern analyses were conducted in R 4.0.4 (R Core Team, 2021).

RESULTS

Burn metrics: Ecoregion scale

At the ecoregion scale, the simulation using the invaded fuelscape resulted in more large fires and area burned, increased fire size, BP, $CBP_{>1.2m}$, and $CBP_{>2.4m}$ compared to the uninvaded simulation; however, many of these differences were relatively small (Table 2, Figure 4). Of all the burn metrics examined, invasion had the greatest

TABLE 2 Summary of burn metrics for the invaded and uninvaded simulations.

Simulation comparisons	Annual no. large fires	Annual area burned (ha)	Fire size (ha)	BP	Area burned at $CBP_{>1.2m}$	Area burned at $CBP_{>2.4m}$
Invaded simulation	25.9	78,199	3017	0.0093 (0–0.050)	3,697,106 ha (54.9%)	748,102 ha (11.1%)
Uninvaded simulation	25.7	76,220	2968	0.0091 (0–0.049)	3,622,070 ha (53.8%)	737,993 ha (11.0%)
Absolute difference	0.2	1979	49	0.0002	75,035 ha	10,109 ha
Percent difference	0.8%	2.6%	1.7%	2.2%	2.1%	1.4%

Note: All values report the mean for the entire ecoregion, including all vegetation types. Large fires were considered to be >100 ha. Values in parentheses for burn probability (BP) are ranges; values in parentheses for conditional burn probability (CBP) are percentages of ecoregion. Absolute difference = invaded – uninvaded. Percent difference = absolute difference/uninvaded × 100. $CBP_{>1.2m}$ and $CBP_{>2.4m}$ indicate the areas of the ecoregion that, if burned, would have flame lengths >1.2 m and >2.4 m, respectively.

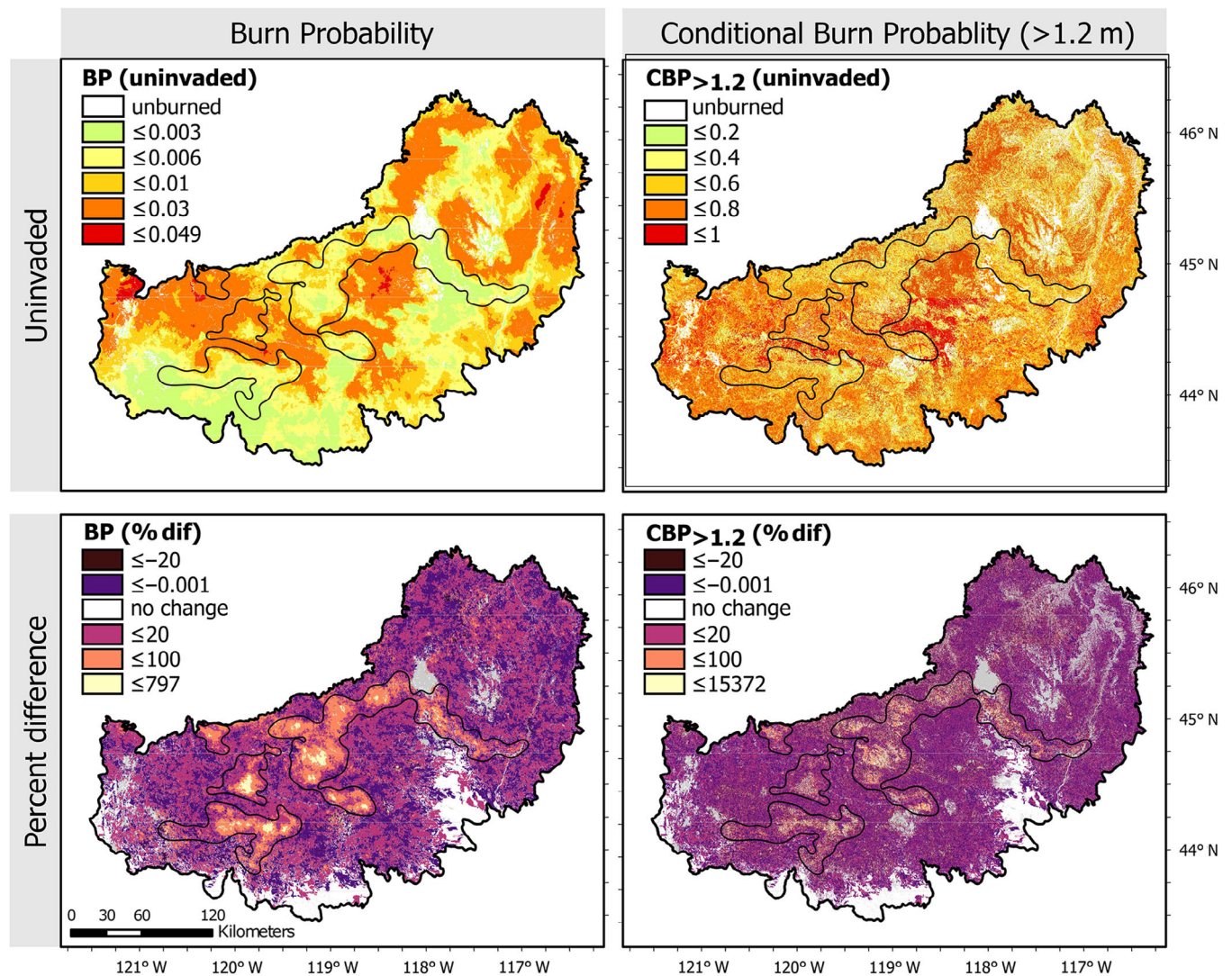


FIGURE 4 Simulated annual burn probability (BP) and conditional probability of burning with flame lengths greater than 1.2 m ($CBP_{>1.2m}$) for the uninverted simulation and percent difference (dif) in fire metrics between the invaded and uninverted simulations $((invaded - uninverted)/uninverted \times 100)$. Positive values show where fire metrics increased with invasion, and negative values represent where fire metrics decreased with respect to the uninverted simulation. Gray shading indicates nonburnable areas. Black polygons outline areas where invasion and reassigned fuel modes presented in Figure 3 are concentrated.

influence on mean annual area burned, increasing it by 2.6% relative to the uninverted simulation (Table 2). More importantly, simulated invasion effects on burn metrics were markedly high within and adjacent to invaded core habitat areas (Figure 4). Within invaded core habitat, where fuel models were altered to reflect invasion (2.8% of the entire study area), mean BP was 0.002 (44.7%) higher, $CBP_{>1.2m}$ was 0.27 (61.8%) higher, and $CBP_{>2.4m}$ was 0.02 (39.0%) higher in the invaded simulation. In invasion-adjacent areas (3 km of invaded area buffer excluding invaded areas), BP was 0.0005 (5.9%) higher, $BP_{>1.2m}$ was 0.009 (1.9%) higher, and $BP_{>2.4m}$ was 0.002 (2.6%) higher than when these same areas were uninverted. Open and closed tree canopy forests collectively made up 57.6% of the invasion-adjacent area.

BP and flame lengths differed by vegetation type, as did the extent to which invasion influenced burn metrics (Figure 5). Mean $CBP_{>1.2m}$ by vegetation type ranged from 0.28 to 0.64, and mean BP ranged from 0.006 to 0.013. For both simulations, mean $CBP_{>1.2m}$ was highest in wetland/riparian areas and closed canopy forests and lowest in recently disturbed areas (Figure 5). Mean BP was highest in closed canopy forests for both simulations. The vegetation types with the lowest mean BP were dwarf-shrublands for the uninverted simulation and recently disturbed areas for the invaded simulation (Figure 5). As noted above, the effect of invasion on mean and median BP and $CBP_{>1.2m}$ for most vegetation types appeared small at the ecoregion scale (Figure 5); however, there was a substantial effect on burn metrics

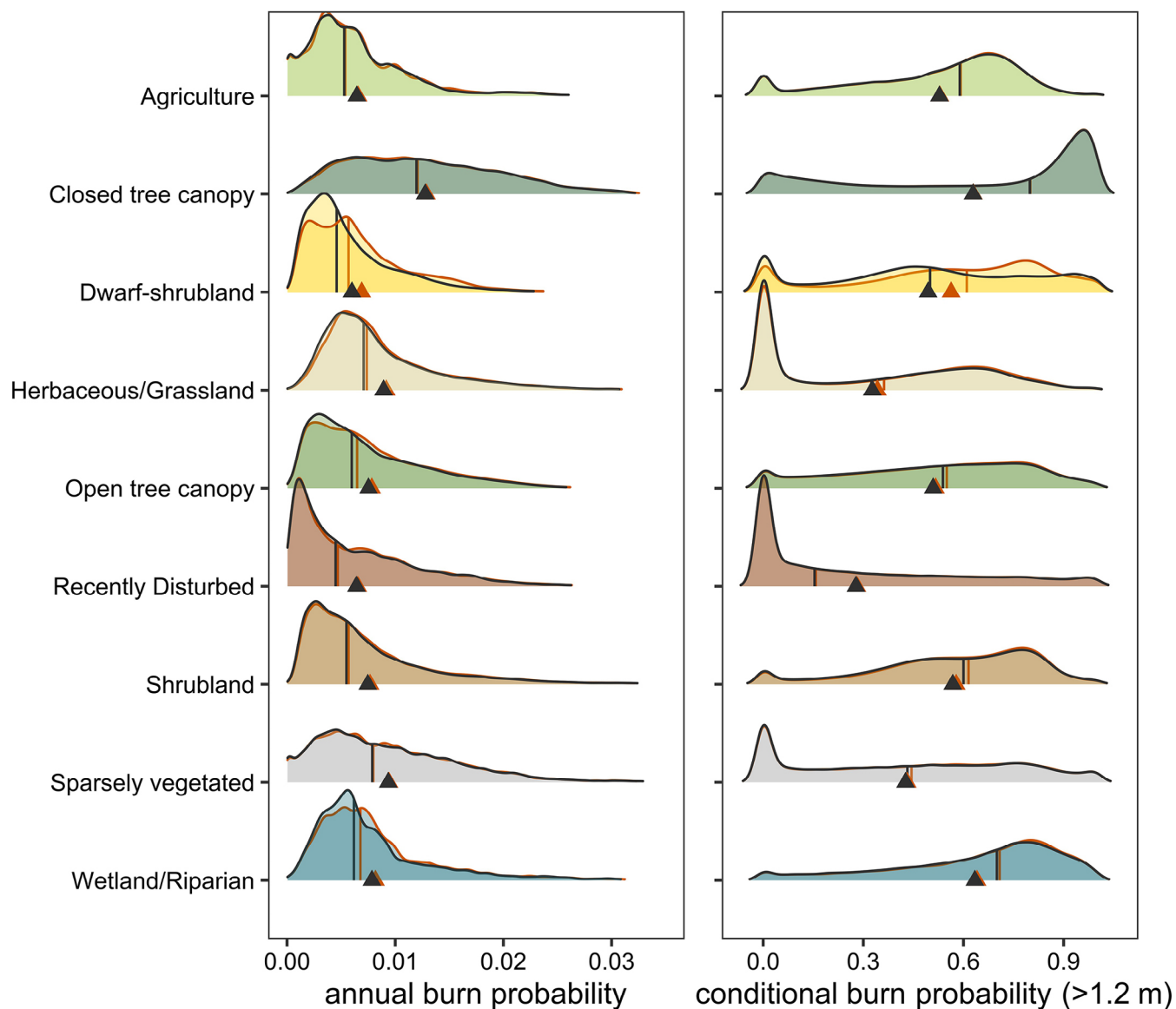


FIGURE 5 Probability density plots of annual burn probability and conditional probability of burning at >1.2 m flame lengths for the uninvasive (black outline) and invasive (orange outline) simulations for each vegetation type. Triangles represent the mean values, and vertical lines represent median values for the uninvasive (black) and invasive (orange) simulations.

in dwarf-shrublands where the invasion was concentrated. Mean BP in dwarf-shrublands was 0.001 (15%) higher, and mean $CBP_{>1.2m}$ was 0.07 (14.0%) higher in the invaded simulation than in the uninvaded (Figure 5).

Fire transmission

Fire transmission between vegetation types differed between the invaded and uninvaded simulations (Figure 6). On average, large fires ignited in dwarf-shrublands spread into and burned 13.7% (308 ha year⁻¹) more of the study area in the invaded simulation. Collectively, these fires

burned 14.5% (43 ha year⁻¹) and 15.4% (72 ha year⁻¹) more closed and open canopy forests, respectively (Figure 6; Appendix S5). Simulated fires ignited in all vegetation types spread into and burned more dwarf-shrubland in the invaded simulation (Figure 6; Appendix S5). However, the greatest increases were from fires ignited in closed and open canopy forests, which spread into and burned 16.5% (76 ha year⁻¹) and 19.9% (132 ha year⁻¹) more dwarf-shrubland in the invaded simulation, respectively. Self-burning in dwarf-shrublands (burned area from fires ignited within the same vegetation type) was 27.5% higher in the invaded simulation compared to the uninvaded simulation.

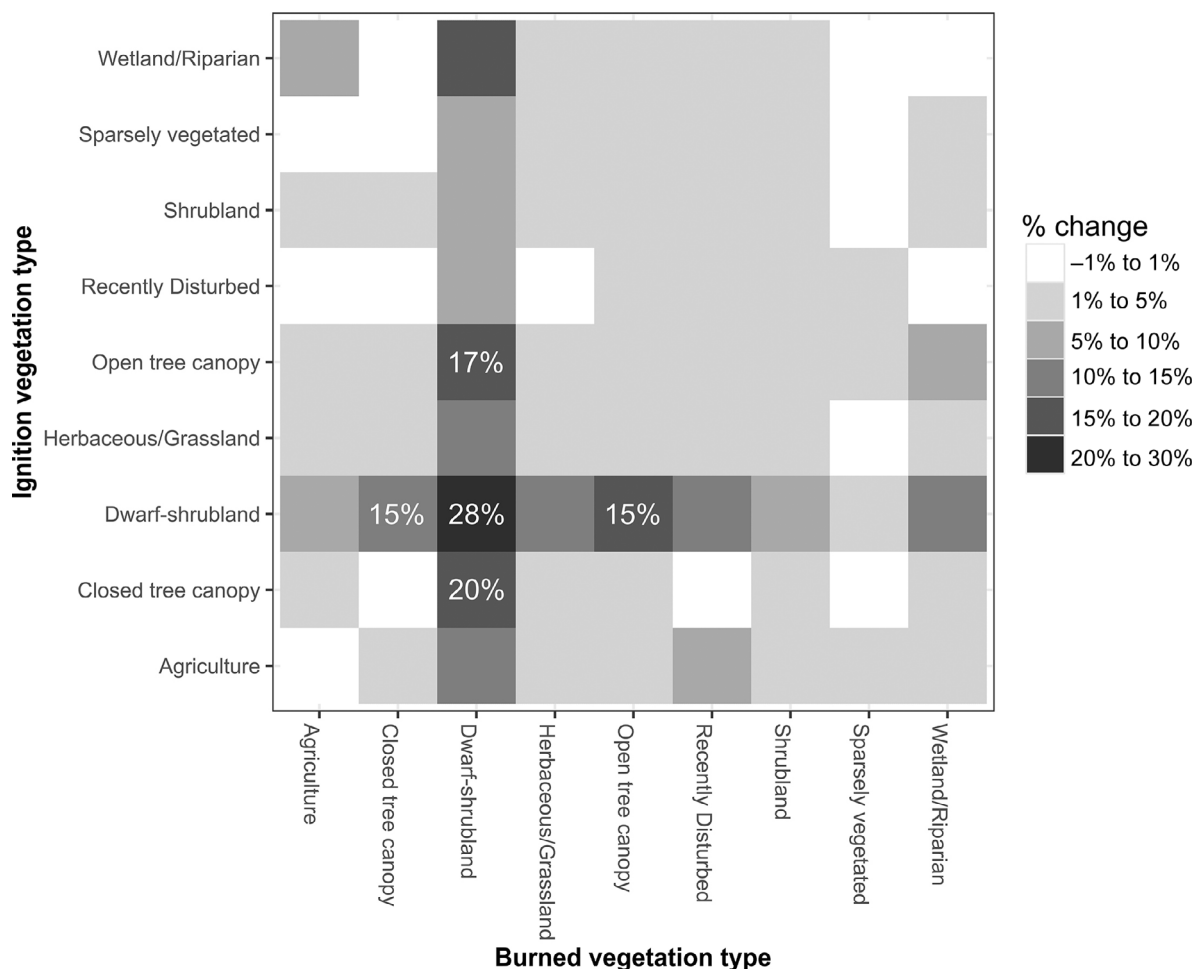


FIGURE 6 Percent change in mean annual area burned between the invaded and uninvaded simulations (absolute difference/uninvaded \times 100) for fires that started within “ignition” vegetation types and spread into “burned” vegetation types.

Spatial patterns of fire: Local forest, patch, and landscape scales

On average, burn metrics in forest cells were influenced by the amount of invaded area in the surrounding neighborhood (Figure 7). Predicted difference in BP, $CBP_{>1.2m}$, and $CBP_{>2.4m}$ in forested cells between the invaded and the uninvaded simulations increased substantially as the amount of invaded area within the surrounding 116.6 ha neighborhood increased (Figure 7). With 25% of the neighborhood invaded, mean BP, $CBP_{>1.2m}$, and $CBP_{>2.4m}$ in focal forested cells were 0.002 (28%), 0.045 (9%), and 0.014 (16%) higher in the invaded simulation, respectively. These differences increased when 50% of the neighborhood was invaded, and mean BP, $CBP_{>1.2m}$, and $CBP_{>2.4m}$ in focal forested cells measured 0.003 (58%), 0.091 (18%), and 0.029 (45%), respectively, higher. In the uninvaded simulation, BP generally decreased in forested cells as the proportion of core habitat in their neighborhood increased; however, when these areas were

invaded, BP remained relatively consistent regardless of increasing invasion in the neighborhood (Figure 7a). These trends were not consistent for $CBP_{>1.2m}$ in forested cells, where predicted $CBP_{>1.2m}$ increased substantially as the proportion of the neighborhood invaded increased in the invaded simulation but remained relatively low when the corresponding core habitat was uninvaded (Figure 7b). See Appendix S6 for summary statistics for all GAMs.

The invaded fuelscape represented patches of continuous invaded core habitat ranging in size from 1.4 to 8650 ha (i.e., 1–6007 pixels). The median and mean invaded patch sizes were 1.4 and 10.7 ha, respectively, with only a quarter of invaded patches measuring larger than 4.3 ha. Mean BP and $CBP_{>1.2m}$ were consistently higher in invaded patches than when these same core habitat areas were uninvaded, and the magnitude of this difference varied according to patch size (Figure 8). With both BP and $CBP_{>1.2m}$, the difference between the invaded and uninvaded simulations increased as the size of the invaded patch increased (Figure 8).

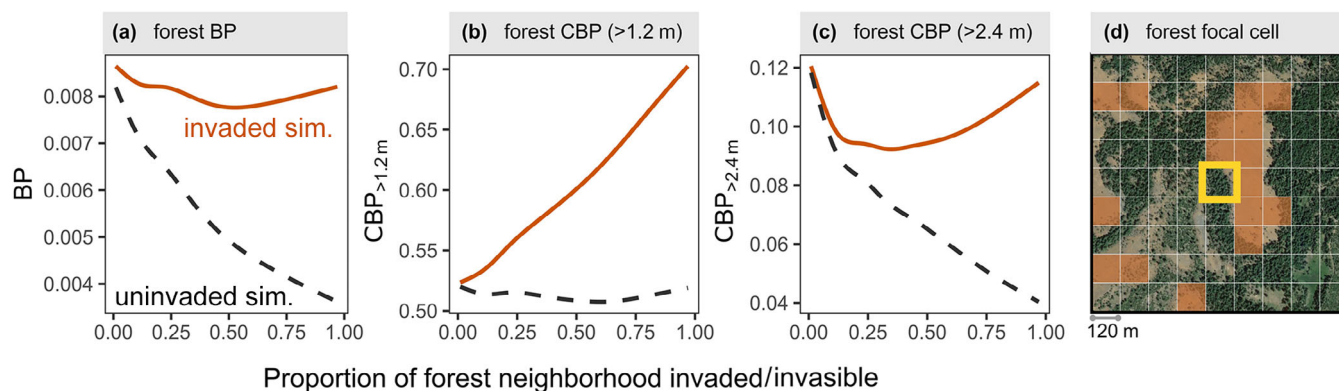


FIGURE 7 Predicted focal forest (a) annual burn probability (BP), (b) conditional probability of burning with flame lengths >1.2 m ($CBP_{>1.2m}$), and (c) conditional probability of burning with flame lengths >2.4 m ($CBP_{>2.4m}$) response to the proportion of invaded neighborhood (with respect to the invaded simulation [sim.]) surrounding forested focal cells ($n = 357,182$). For example, with 25% of the neighborhood invaded, mean BP was 0.002 (29%) higher than in the same forested cell when the neighborhood was uninvaded. (d) An example focal forest cell (outlined in yellow) and 116.6 ha neighborhood with invaded cells shaded orange. Response curves were generated using generalized additive models with a binomial family.

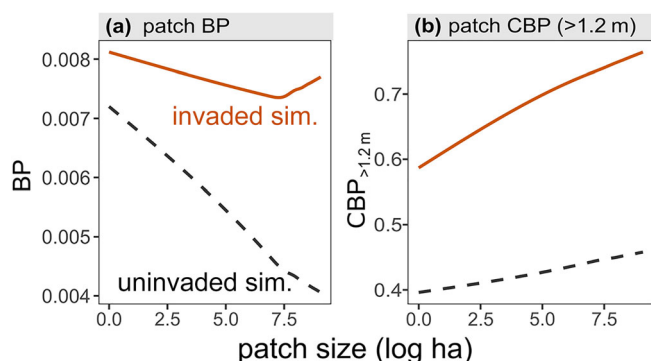


FIGURE 8 Predicted mean (a) annual burn probability (BP) and (b) conditional probability of burning with flame lengths >1.2 m ($CBP_{>1.2m}$) for invaded core habitat patches and corresponding areas in the uninvaded simulation (sim.) in response to patch size ($n = 17,783$). For example, with a patch size of 2.5 log ha (12 ha), mean patch BP was 0.0014 (23%) higher than in the same area when uninvaded. Response curves were generated using generalized additive models with a binomial family.

In invaded patches, BP decreased slightly with increasing patch size, but this trend was much stronger in these same core habitat patches when uninvaded (Figure 8a). This suggests that patch size does not strongly influence BP given continuous fuels, but that uninvaded patches may act as barriers to fire spread by reducing inner patch burning with increasing patch size. In the uninvaded simulation, predicted $CBP_{>1.2m}$ remained consistently below 0.46 regardless of patch size, but ranged from 0.6 to 0.76 when the same patches were invaded, demonstrating that invaded patches are much more likely to experience flame lengths above 1.2 m when burned (Figure 8b) and could require a shift from direct to indirect fire management practices.

Landscape-scale burn metrics were heavily influenced by the proportion of the landscape invaded (Figure 9). With 25% of the landscape invaded, predicted landscape BP, $CBP_{>1.2m}$, and $CBP_{>2.4m}$ were 0.002 (29%), 0.098 (21%), and 0.009 (17%) higher in the invaded simulation than the uninvaded simulation, respectively. The difference in predicted landscape BP between the invaded and uninvaded simulations increased with increasing proportion of the landscape invaded until the proportion invaded exceeded 75% (Figure 9a). As invasion exceeded 75% of the landscape, the difference in landscape BP declined, likely because dwarf-shrublands often have lower BP than closed canopy forests, even when invaded (Figure 5). In contrast, the difference in landscape $CBP_{>1.2m}$ and $CBP_{>2.4m}$ generally increased as the landscape became saturated with invasion (Figure 9b,c), indicating that landscape-scale flame lengths are likely to continue increasing with invasion extent even when BP does not.

DISCUSSION

The extent to which the ventenata invasion influenced simulated fire in the BME varied depending on the degree of invasion. As expected, the relatively small extent of reassigned fuel models reflecting invasion (2.8% of the entire ecoregion) resulted in modest shifts in fire behavior at the ecoregion scale. However, we saw substantial increases in BP and conditional probability of burning at moderate and high flame lengths with increasing invasion when considering individual forest cells, nonforest patches, and smaller landscapes (~100 ha).

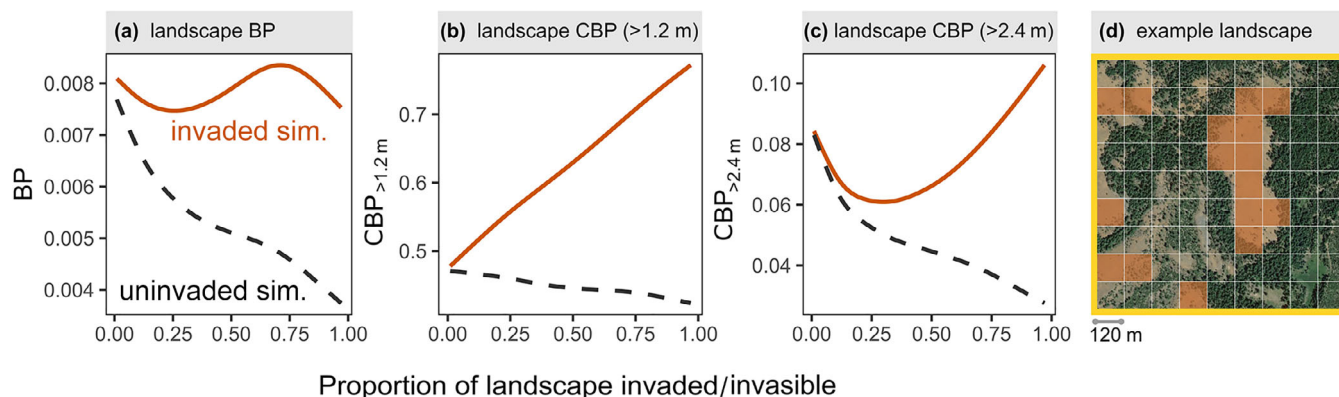


FIGURE 9 Predicted landscape (a) annual burn probability (BP), (b) conditional probability of burning with flame lengths >1.2 m (CBP _{$>1.2m$}), and (c) conditional probability of burning with flame lengths >2.4 m (CBP _{$>2.4m$}) responses to the proportion of landscape invaded/corresponding core habitat areas in the uninvaded simulation (sim.). Landscape burn metrics were averaged across each 116.6 ha landscape ($n = 789,062$). For example, when 25% of the landscape was invaded, mean BP was 0.002 (29%) higher than when the same landscape was uninvaded. (d) An example landscape with invaded cells shaded orange. Response curves were generated using generalized additive models with a binomial family.

The greatest impacts on BP and flame lengths occurred within large, invaded patches (primarily dwarf-shrublands) and nearby forests, where increased fine fuel loads facilitated fire spread between dwarf-shrublands and the surrounding forested landscape. These results suggest that, despite invading primarily nonforested patches (Tortorelli et al., 2020), annual grass invasion can alter fire behavior and fire management practices across forest-mosaic landscapes where invasion serves as a vector connecting areas of higher fuel loads.

Invaded dwarf-shrublands heavily impacted

As expected, *ventenata* was most concentrated and had the greatest impact on fire in dwarf-shrublands, where increased fine fuel loading resulted in higher BP and conditional flame lengths. Our findings closely reflect those from observational studies in other western shrub and desert ecosystems with historically infrequent and patchy fire, where invasive grasses increased area burned, fire frequency, and flame lengths in invaded areas (Balch et al., 2013; Bradley et al., 2017; Fusco et al., 2019).

Dwarf-shrublands support a diverse floral community with many rare and endemic species and provide important habitat for wildlife, including endangered sage-grouse, and winter forage for elk and deer (Johnson & Swanson, 2005). Increased BP may lead to shortened fire return intervals and altered fire regimes in invaded areas given that, like many invasive grasses, *ventenata* is known to recover quickly after fire (Tortorelli et al., 2020). Such “grass-fire-cycles” can functionally

remove established native species and regenerating seedlings that are not adapted to survive or recover quickly after fire (Mahood & Balch, 2019), leading to state shifts (D’Antonio & Vitousek, 1992) and the loss of ecosystem functions, including hydrologic (Turnbull et al., 2012) and nutrient cycling (Mahood et al., 2022; Nagy et al., 2021), wildlife habitat, and soil stability (Bowker et al., 2004).

Across the forest mosaic, invasion impacts increased with increasing patch size, suggesting that larger invaded areas (primarily dwarf-shrublands) may be at higher risk for altered fire regimes and potential type conversions. This is consistent with studies examining the effectiveness of woody fuel treatments on modeled fire behavior that found treatment size and the proportion of interior area to edges to be an important factors influencing exposure to fire (Arkle et al., 2012; Finney et al., 2005; Prichard et al., 2020; Prichard & Kennedy, 2014). However, in this case, uninvaded patches acted as natural fuel treatments, buffering fire-sensitive vegetation from the surrounding forested matrix and slowing landscape fire transmission. In contrast, invaded patches enhanced fire flow, facilitating burning of fire-sensitive areas and promoting landscape fire spread.

Invasion facilitates landscape-scale fire spread

Invasion in nonforest patches facilitated fire spread across the landscape, with increased fire transmission primarily occurring into and between forested areas. These findings reflect observational and simulation studies in other ecosystems demonstrating that invasive grasses can contribute

to fire spread between invaded and uninvaded vegetation types (Balch et al., 2009; Ellsworth et al., 2014; Gray & Dickson, 2016). For example, patches of cheatgrass contributed to simulated landscape-scale fire spread across a mixed pinyon-juniper woodland and shrub-steppe landscape (Gray & Dickson, 2016). Within the 48,500 ha northern Arizona study area, increased fire spread led to higher burn probabilities and flame lengths in nearby woodlands (Gray & Dickson, 2016). In this study, woodlands with high proportions of invasion in their surrounding neighborhood (e.g., ecotones) were more likely to burn and, if exposed to fire, were more likely to burn at high intensity than when nearby core habitat patches were uninvaded (Gray & Dickson, 2016).

Within the extensive BME, even moderate invasion of the surrounding landscape (e.g., 20%) substantially increased landscape-scale BP and conditional flame lengths compared to the uninvaded landscape. Our findings are consistent with findings from fuel-reduction treatment studies where treatments reduced modeled landscape-scale fire occurrence and flame lengths with relatively low proportions of the landscape treated (Ager et al., 2010; Collins et al., 2011, 2013; Moghaddas et al., 2010). Although, here, invasion acted as the reverse of a fuel treatment by increasing fuel loads in previously fuel-limited areas. These results demonstrate the ability of the *ventenata* invasion to influence landscape-scale BP and fire behavior despite primarily invading nonforested areas and a relatively small proportion of the ecoregion. Our findings are especially alarming given that *ventenata* has yet to meet its full invasion potential, and is predicted to become more abundant and widespread throughout the study area and across the American West (Jones et al., 2018; Jarnevich et al., 2021; Nietupski, 2021). Furthermore, we did not consider the effects of *ventenata* invasion on fuel or fire behavior where it invaded areas outside of *ventenata*'s core habitat layer (an additional 4.9% of the ecoregion), including within more productive grasslands, shrublands, and open canopy forests, or where cheatgrass invasion was likely to have already altered fuel loads. Despite these vegetation types supporting more abundant fine fuels than dwarf-shrublands, higher fuel loads owing to *ventenata* invasion could increase flammability and continuity, further altering fire behavior across the region.

Increases in BP and fire frequency could have different ecological implications for forests than historically fire-resistant vegetation types. Given that many forests are in a state of fire deficit, more frequent low-severity fire may have desirable forest health outcomes, including robust and diverse native herbaceous vegetation and thinning of smaller trees and species less tolerant of fire (Agee, 1993; Hessburg et al., 2015). However, our results suggest that invasion may contribute to increased flame

lengths and crown fire in nearby forests, which could result in higher amounts of canopy loss when burned (Ager et al., 2010, 2014). In addition, invasion following canopy loss in forests may negatively impact understory native plant communities and forest recovery, as has been documented with invasion following fire in nonforested ecosystems (Peeler & Smithwick, 2018; Reilly et al., 2020; Tortorelli et al., 2020).

Even moderate reductions in canopy cover can create suitable conditions for annual grass invasion in forests, potentially expanding invasive annual grass distributions and exacerbating annual grass impacts (Kerns et al., 2020; Peeler & Smithwick, 2018; Reilly et al., 2020). For example, *ventenata* is known to invade forests with up to 40% canopy cover and has heavily invaded burned forests following canopy loss (Nietupski, 2021; Tortorelli et al., 2020). Fire-induced canopy reductions to under 30% promoted cheatgrass invasion in a Californian montane forest (Peeler & Smithwick, 2018). Aside from fuel changes, invasive species can limit forest recovery if tree seedlings are outcompeted by invasive species that readily colonize after fire, even if climate and site conditions are favorable for establishment (Davis et al., 1998; Flory et al., 2015). Competitive effects may be intensified by drought stress, either exogenous or from dry postfire conditions, if invasives are more tolerant than regenerating tree seedlings (Welles & Funk, 2020). This may be especially problematic for forest edges, which already exist in less suitable climate conditions (Parks et al., 2019), adding to concerns about transformations after high-severity fire in forest ecosystems (Coop et al., 2020; Krosby et al., 2020; Parks et al., 2019).

Climate change is likely to exacerbate invasion-fire dynamics in many forest types. Low-elevation, dry, open forests that experience more frequent fire are currently at the highest risk for invasion (Crawford et al., 2001; Peeler & Smithwick, 2018) and subsequent type conversions (Coop et al., 2020; Parks et al., 2019; Syphard et al., 2022). These conditions are predicted to expand as temperatures rise and precipitation becomes more variable (Davis et al., 2020). Furthermore, climate change is expected to lengthen fire seasons and increase disturbance activity across western forests (Abatzoglou & Williams, 2016; Westerling, 2016). This could include larger areas of high-severity fire in forests, which may provide favorable conditions for invasion (Reilly et al., 2020) and short-interval reburns (Kerns et al., 2020). Increased drought and fire in future landscapes may further facilitate invasion-fire feedbacks and lead to landscape-scale state shifts from forests to annual grasslands (Coop et al., 2020; Keeley et al., 2011; Kerns et al., 2020). Future modeling work may consider investigating these ideas by combining state-and-transition, fire, and climate models, as with the

landscape model Envision (Barros et al., 2018; Bolte et al., 2006; Spies et al., 2017) or LSim (Ager et al., 2017), which integrates FSim fire modeling with the Forest Vegetation Simulator (FVS; Crookston, 2014).

Management implications

Increased burn probabilities and flame lengths as a result of invasion may influence fire and fuel management strategies throughout the ecoregion and beyond. The loss of fire-resistant patches from forest mosaics could limit firefighter access points and safety zones (Hallmark & Romero, 2015), and higher flame lengths may require additional and/or different resources to manage, thus limiting resources elsewhere. In invaded dwarf-shrublands, fires were likely to transition from low to moderate flame lengths when burned (flame lengths exceeding 1.2 m) regardless of invaded patch size. This increase would require a shift in fire management and suppression practices from persons using hand tools to large machinery or aerial retardant (Andrews & Rothermel, 1982). Shifts from surface to crown fires in forests were less likely, given that wildfires in forests generally have higher flame lengths than shrublands to begin with. However, forests in the vicinity of invaded areas may still experience shifts in flame lengths from surface to crown fire in some cases. Such shifts could put additional pressure on already limited equipment and human resources, further complicating fire management practices. Additionally, introducing machinery into invaded areas increases opportunities for propagules to spread into uninvaded areas, potentially exacerbating invasion and future impacts (Brooks, 2008). Finally, increased ignitability of nonforest patches due to an abundance of highly flammable fuels frequently occurring close to roads could result in an increase in the number of lightning and human ignitions that grow into fires requiring management decisions (Fusco et al., 2019).

Thinning of forests through mechanical treatments and/or fire is a common management objective for creating and maintaining resilient forest structure in western dry conifer forests (Agee & Skinner, 2005; Hessburg et al., 2015). Although our study did not investigate the influence of fuel treatments on fire per se, many parallels can be drawn between abundance and configuration of grass invasions to studies examining the effectiveness of woody fuel treatments on modeled fire occurrence and behavior in forests. Reduction of fine fuels within nonforest patches—represented by the uninvaded fuelscape—may have similar effects to treating woody fuels across a forested landscape. For example, many woody fuel reduction studies in western forests reported substantial decreases in simulated BP and potential flame

lengths within treated areas, but the effects of treatment diminished as the proportion of the landscape treated decreased and fewer fires intersected the treated area (Collins et al., 2011; Moghaddas et al., 2010; Thompson et al., 2013, 2017). In a simulation study in northern California with nearly 10% of the landscape treated, fuel treatments reduced BP over 60% in treated areas and between 17% and 36% in nearby untreated areas (Moghaddas et al., 2010). Additionally, crown fire was reduced within treated areas, but these effects did not extend to the surrounding landscape (Moghaddas et al., 2010). These findings are comparable to results from our study, where BP and conditional flame lengths were, respectively, 45% and 39% higher within invaded areas but varied considerably within uninvaded (i.e., untreated) areas depending on the extent of nearby invasion.

Current fuel reduction treatments and associated studies in western forests rarely consider how invasive annual grasses contribute to posttreatment fire behavior. Incorporating weed management practices as fuel treatments could help meet management objectives in invaded forests, along forest ecotones, and in forest mosaics where fires are likely to ignite in invaded areas and spread into/between adjacent forests. It is important to note that the duration and effectiveness of weed-oriented herbicide treatments without intensive restoration efforts is relatively short (e.g., 1–4 years; Elseroad & Rudd, 2011), whereas woody fuel treatment effectiveness often lasts over five years (Kalies & Yocom Kent, 2016; Prichard et al., 2020). Invasive grassy fuel management requires increased focus in areas where natural fuel breaks have been compromised and fire management strategies have been altered due to invasion.

CONCLUSIONS

Our study is the first large-scale ecoregional analysis of the impact of an invasive annual grass on simulated fire behavior in western forest ecosystems and demonstrates that annual grass invasion can influence landscape-scale fire, despite primarily invading relatively small nonforested patches. Substantial increases in BP and flame lengths within invaded areas and nearby forests due to increased fire spread may lead to shifts in fire suppression practices, strain already limited resources, and impact native plant communities and wildlife habitat. Grass invasions could have implications for forest and biodiversity loss as forest patches become surrounded by invasion and postfire forest recovery is inhibited by competitive grasses. Additionally, given that invasion and fire are expected to be exacerbated by climate change, we expect these issues to become increasingly prominent in the future. While our study

focused on a single species invasion in the Inland Northwest, we hope to set the stage for additional work focused on the impacts of invasive species on fuels and fire behavior at landscape scales. In addition, results from our simulations can be applied to better understand what and how human and natural resources, such as communities and the wildland–urban interface, at-risk species, water sources, soils, and other highly valued resources or assets may be affected by invasion and altered fire behavior.

AUTHOR CONTRIBUTIONS

All authors contributed to study design. Kevin C. Vogler, Alex Dye, John B. Kim, Rebecca Lemons, Michelle Day, Ty C. Nietupski, and Claire M. Tortorelli assisted in creating data layers and running fire simulations in FSim. Claire M. Tortorelli curated and analyzed the data. Claire M. Tortorelli wrote the original draft, and all authors contributed substantially to review and editing of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or relationships that influenced the work reported here.

DATA AVAILABILITY STATEMENT

Novel code for all analyses (Tortorelli, 2023) is available from Zenodo: <https://doi.org/10.5281/zenodo.7516577>. Data (Tortorelli, 2022) are available from OSF: <https://doi.org/10.17605/OSF.IO/9AWTS>.

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SUPPORTING INFORMATION

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

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