esa

ECOSPHERE

Rain-shadow forest margins resilient to low-severity fire and climate change but not high-severity fire

LUCAS B. HARRIS[1,†] AND ALAN H. TAYLOR[2]

[1]*Department of Geography, The Pennsylvania State University, 302 Walker Building, University Park, Pennsylvania 16802 USA*
[2]*Department of Geography, Earth and Environmental Systems Institute, The Pennsylvania State University, 302 Walker Building, University Park, Pennsylvania 16802 USA*

Citation: Harris, L. B., and A. H. Taylor. 2020. Rain-shadow forest margins resilient to low-severity fire and climate change but not high-severity fire. Ecosphere 11(9):e03258. 10.1002/ecs2.3258

Abstract. At semi-arid forest margins, increasing climatic stress combined with disturbances like wildfire threatens to cause widespread forest loss. However, forest resilience is likely to vary over gradients of topoclimate and vegetation characteristics, and the influences of local climate and tree species on tree regeneration remain key uncertainties in assessing forest recovery from wildfire. We surveyed tree regeneration 9–15 yr post-fire at 397 gridded field plots across four sites at a lower montane forest-steppe ecotone in the eastern Sierra Nevada, California, USA, and then used statistical modeling to characterize how the probability of tree regeneration presence for different species varied along gradients of fire severity, topoclimate, and post-fire vegetation structure and composition. Tree regeneration was absent in half the field plots, and only 19% of plots contained >250 seedlings and saplings per ha, suggesting potential for regeneration failure and forest loss. Tree regeneration composition was consistent with shifts away from Jeffrey pine (*Pinus jeffreyi*) and toward drought-tolerant pinyon pine (*P. monophylla*) and mountain mahogany (*Cercocarpus ledifolius*). Tree regeneration was strongly associated with trees that survived fire indicating tree cover is crucial to buffer establishment against climatic stress. Based on projected future water balance, the likelihood of tree regeneration at these sites does not decline substantially by the end of the century. Consequently, these forests appear to be resilient to climate change under a low-severity fire regime, but large patches of high-severity fire are likely to shift vegetation away from forest. Our results highlight the importance of facilitation and future water balance in maintaining semi-arid forest margins that burn at low severity while high-severity fire threatens to convert forest to steppe or invasive grasslands.

Key words: climate change; ecotone; fire severity; tree regeneration; vegetation switching; wildfire.

Received 3 April 2020; revised 18 June 2020; accepted 24 June 2020; final version received 11 August 2020. Corresponding Editor: Franco Biondi.

Copyright: © 2020 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** lbh146@psu.edu

INTRODUCTION

Forest ecosystems worldwide are changing rapidly in response to a warmer and drier climate as well as altered land use and disturbance regimes (Allen et al. 2010). Over the next century, modeled interactions between climate and wildfire indicate significant potential for widespread forest loss (Miller et al. 2018, Serra-Diaz et al. 2018) and geographic shifts in tree recruitment and tree species composition (Liang et al. 2017). Disturbances are likely to be key triggers of future forest loss where climate change reduces the likelihood of tree establishment (Jackson et al. 2009, Dobrowski et al. 2015, Stevens-Rumann et al. 2018, Kemp et al. 2019). Lower-elevation or trailing-edge forest margins in semi-arid ecosystems are at particularly high risk of fire-catalyzed forest loss because this is where conditions are already marginal for tree

establishment and survival (Parks et al. 2019). Despite growing interest in post-fire tree regeneration and its drivers, assessments of spatial variability in tree regeneration and fire-driven compositional shifts remain pressing research needs (Stevens-Rumann and Morgan 2019).

Recent studies of post-fire tree regeneration in the western United States suggest that climatic thresholds (e.g., in summer temperatures, soil moisture, and moisture deficit) for regeneration exist and that recovery of low-elevation forests following stand-replacing fire under warming and drying conditions is unlikely (Stevens-Rumann et al. 2018, Kemp et al. 2019, Davis et al. 2019*a*). Climate could become an increasingly dominant influence on post-fire patterns of tree regeneration as climatic thresholds are exceeded over larger areas (Tepley et al. 2017, Stevens-Rumann et al. 2018, Kemp et al. 2019, Davis et al. 2019*a*).

Measures of water balance integrate climate, terrain, soil properties, and seasonal climatic variability and are therefore particularly well-suited to evaluate climatic influences on tree distribution patterns and tree regeneration (Stephenson 1998, Lutz et al. 2010, Petrie et al. 2016, Rodman et al. 2019). Water balance may be divided into two components, actual evapotranspiration (AET) and climatic water deficit (CWD; Stephenson 1990, Flint et al. 2013). AET is a measure of the simultaneous availability of water and energy for plant growth, summed over time, and is a variable that controls net primary productivity (Rosenzweig 1968, Stephenson 1990). CWD is potential evapotranspiration minus AET, or the difference between evaporative demand and available water, and is considered a measure of drought independent of natural vegetation (Stephenson 1990). This water balance framework is particularly useful for studies of vegetation dynamics because it partitions productivity as driven by water and energy fluxes (AET) from drought intensity (CWD; Stephenson 1998). In the context of tree regeneration in a Mediterranean climate region, AET represents the availability of moisture to drive seedling establishment and growth primarily in the spring and early summer whereas CWD represents drought intensity primarily in the summer and fall which could cause seedling mortality.

California's forests present an interesting case from a water balance perspective since, unlike most other Mediterranean climate regions worldwide, mean annual precipitation and consequently AET may increase in parts of California by the end of the century due to increasing winter precipitation (Polade et al. 2017, Pierce et al. 2018). Thus, tree populations able to survive greater summer drought intensity may maintain or even expand their range if they can take advantage of potential additional moisture in the winter and spring. In such systems where climate change may not be exerting a strong directional influence on tree regeneration, maintaining tree cover may hinge on avoiding disturbance regime changes (e.g., low severity to high severity) which can trigger vegetation switching (Johnstone et al. 2016).

Fine-scale variation in topoclimate over complex terrain can also strongly influence tree regeneration and a forest's capacity for post-disturbance recovery, an effect identified by studies of local tree establishment in environmental microrefugia (Ashcroft et al. 2012, Davis et al. 2016, Lenoir et al. 2017, McLaughlin et al. 2017). In moisture-limited systems particularly, tree regeneration can be restricted to topoclimatic settings with higher moisture availability and lower drought stress. Moreover, tree establishment can also be episodic and related to unusually wet years, and climatic warming and drying may reduce future opportunities for tree establishment both temporally and spatially (Brown and Wu 2005, Jackson et al. 2009, Savage et al. 2013, Davis et al. 2016).

The buffering effects of vegetation cover on local climate and water balance further influence tree regeneration by mediating the effects of regional climate change (Franklin et al. 2016, Lenoir et al. 2017, Shive et al. 2018, Davis et al. 2019*b*). Trees and shrubs provide shade, moderate temperature, and soil moisture; affect nutrient cycling; and sometimes protect seedlings from herbivory (Chen et al. 1999, Chambers 2001, Gómez-Aparicio et al. 2004, Davis et al. 2019*b*). Due to these effects and the need for nearby seed sources, forests may be unable to recover following moderate–high-severity fire that removes tree and shrub cover (Savage and Mast 2005, Chambers et al. 2016). Additionally, loss of forest cover from severe fire may encourage invasion of annual grasses such as cheatgrass (*Bromus tectorum*) which create continuous and

highly flammable fine fuel beds that can dramatically increase fire frequency preventing tree establishment (Brooks et al. 2016).

Individual tree species respond differently to the altered vegetation and climate of post-fire environments, potentially leading to community reshuffling (Harvey et al. 2016). Species such as ponderosa pine (*Pinus ponderosa*) or Jeffrey pine (*P. jeffreyi*) with thick bark can survive low–moderate severity fires. In contrast, species with thin bark such as singleleaf pinyon pine (*P. monophylla*) avoid fire and are often confined to fire-safe areas, or rocky sites with insufficient fuels to carry a surface fire (Geldenhuys 1994, Burwell 1998, Miller and Tausch 2001). Recently, fire-avoiding tree species have expanded into more mesic and fire-exposed areas due to fire exclusion, which creates a novel juxtaposition of fire-resistant and fire-avoiding tree species, elevates fire hazard, and creates potential for future range shifts in tree species distributions in response to disturbance (Allen and Breshears 1998, Miller et al. 2008).

Analyses spanning gradients of topoclimate, fire severity and vegetation structure and composition are vital to understanding landscape-scale patterns of forest recovery and forest loss following wildfire. Here, we characterize the effects of topoclimate, local vegetation, and fire severity on post-fire tree regeneration 9–15 yr following wildfire across four sites at semi-arid forest margins on the eastern Sierra Nevada (ESN), California, USA. There is a strong increasing trend in area burned and area burned at high severity across the ESN (i.e., 1984–2017), which suggests a potential shift in disturbance regime (Harris 2019). The Sierra Nevada casts a strong rain shadow, and the ESN escarpment is steep and topographically complex with highly contrasting topoclimatic and vegetation gradients, making it an ideal place to examine local and mesoscale influences on post-fire tree regeneration and how patterns may shift under a changing climate. We addressed four particular questions in this analysis:

1. Is fire triggering forest loss at the forest-steppe ecotone, and if so in what locations? Based on other analyses of post-fire tree regeneration in the western United States, we expected tree regeneration failure consistent with forest loss, particularly in areas of high-severity fire (Savage and Mast 2005, Donato et al. 2016, Welch et al. 2016).
2. Is fire generating a compositional shift in tree species? We expected that regeneration of more drought-tolerant species would be relatively more abundant, consistent with upslope migration of drought-tolerant tree species observed at forest–woodland ecotones (Kelly and Goulden 2008, Minott and Kolb 2020).
3. Do live tree and shrub cover enhance post-fire tree regeneration? We expected that nearby live trees would be crucial for tree regeneration by moderating local climate and providing seed source, and that shrub cover might further encourage regeneration by providing shade and nutrients (Chen et al. 1999, Chambers 2001, Ziffer-Berger et al. 2014).
4. Does variability in water balance over complex terrain influence tree regeneration? If so, how might tree regeneration patterns change by the end of the century? We expected that tree regeneration would respond positively to moisture availability (e.g., AET), and negatively to drought intensity (e.g., CWD; Petrie et al. 2017, Rodman et al. 2019, Davis et al. 2019*a*). Because precipitation may increase at these sites in the future along with temperature, we were uncertain whether water balance trends would increase or decrease the potential for tree regeneration.

Methods

Vegetation gradient and fire history

The ESN contains a characteristic gradient of vegetation types that roughly follows gradients in climate and water balance. Vegetation at the lowest elevations is desert steppe and dominated by sagebrush (*Artemisia tridentata*). Upslope is a woodland belt dominated by singleleaf pinyon pine (*Pinus monophylla*). Western juniper (*Juniperus occidentalis*) in some cases is also present at the lower treeline and may also be found scattered among the higher elevation forests. Curl-leaf mountain mahogany (*Cercocarpus ledifolius*) is also found interspersed near the lower forest

ecotone, especially in rocky areas. Upslope of the steppe and woodland is a belt of yellow pine (i.e., Jeffrey pine or ponderosa pine) forest. In the central and southern Sierra Nevada Jeffrey pine is the dominant, although farther north Jeffrey pine mixes and sometimes hybridizes with the closely related ponderosa pine (Safford and Stevens 2017). Upslope of yellow pine forest, other tree species such as white fir (*Abies concolor*) mix with yellow pine and form mixed-conifer forest.

Tree species on the ESN evolved with and are adapted to different fire regimes. Fire history studies indicate that fire-resistant Jeffrey pine forests on the ESN historically burned frequently (every 2–17 yr) at predominantly low–moderate severity (Stephens 2001, Taylor 2004, Moody et al. 2006, Gill and Taylor 2009, North et al. 2009, Vaillant and Stephens 2009). In contrast, fire-intolerant pinyon pine, mountain mahogany, and western juniper tended to burn infrequently (often >100-yr fire return intervals) and at predominantly moderate–high severity (Wangler and Minnich 1996, van de Water and Safford 2011, Kitchen 2012). Due to these differences in fire tolerance and environmental preferences, regeneration of the tree species of the ESN would be expected to respond differently to different topoclimatic and vegetation drivers (Appendix S1: Table S1).

Study area

Four study sites were chosen to study tree regeneration in the central and southern ESN (Fig. 1) based on three criteria. First, the sites included the vegetation transition in over ~1 km from shrub steppe through Jeffrey pine to mixed Jeffrey pine-white fir forest. Second, all had burned in wildfires 9–15 yr prior (Table 1). Third, all had experienced a range of fire severities that included low-, moderate-, and high-severity effects. The dimensions of the sites were not fixed but instead adjusted so that each site met the above criteria. The two northern sites were located ~8 km apart in the Toiyabe National Forest within the perimeter of the 2002 Cannon Fire (Table 1). Similarly, the two southern sites were located ~9 km apart on the Kern Plateau in the Inyo National Forest, but within different burns (Table 1). Mean annual precipitation at the individual sites ranged from 422 to 578 mm and mean monthly temperatures ranged from −2°–0°C in January to 15°–18°C in July. There was some variation in tree species composition among the sites. For example, pinyon pine was more common at the two northern sites, while mountain mahogany was more common at the southern sites (Appendix S1: Fig. S1).

The field sites likely experienced grazing of sheep and later cattle beginning in the mid-late 19th century, although only the two southernmost sites are in active grazing allotments (Stephens et al. 2004). Nearby settlement and mining activity at the northern sites may have led to logging in the 1800s or early 1900s (Kersten 1964, Gruell 1999), but there was no field evidence of past logging (e.g., cut stumps) at either field site as there usually is in early cut forests in the ESN (Taylor 2004).

Field data

To characterize post-fire vegetation and tree regeneration, we measured vegetation at the four sites from June to September 2017 (Table 1). At each site, vegetation was measured in ~100 plots on a grid with 90 m spacing. Tree diameters (diameter at breast height, dbh) and species were recorded for all live and standing dead trees (>5 cm dbh) in a circular plot of 707 m^2, and distance from the plot center to the nearest live Jeffrey pine >5 cm dbh was measured. Tree seedlings (0.30–1.4 m tall) and saplings (>1.4 m tall, ≤5 cm dbh) were tallied in a nested circular plot of 177 m^2 and recorded by species. Ground cover in the smaller circular plot was estimated by cover class (0%, <1%, 1–5%, 5–25%, 25–50%, 50–75% or >75%) for rock, shrubs, and cheatgrass (*Bromus tectorum*). Because litter depth can influence tree regeneration (Chambers 2001, Ibáñez and Schupp 2002, Legras et al. 2010), we also measured litter depth in each plot. From the plot center, a 20-m transect was established for a random azimuth and a second transect was established by subtracting 120°. Litter depth was measured at 5, 9, and 13 m from the plot center, and the average litter depth for a plot was determined from those six measurements.

To further characterize vegetation, we calculated the basal area (BA, m^2/ha) by tree species and identified the species with the highest basal area as the dominant tree species for each plot. Similarly, the genus of the shrub with the highest cover was also assigned to each plot to create a

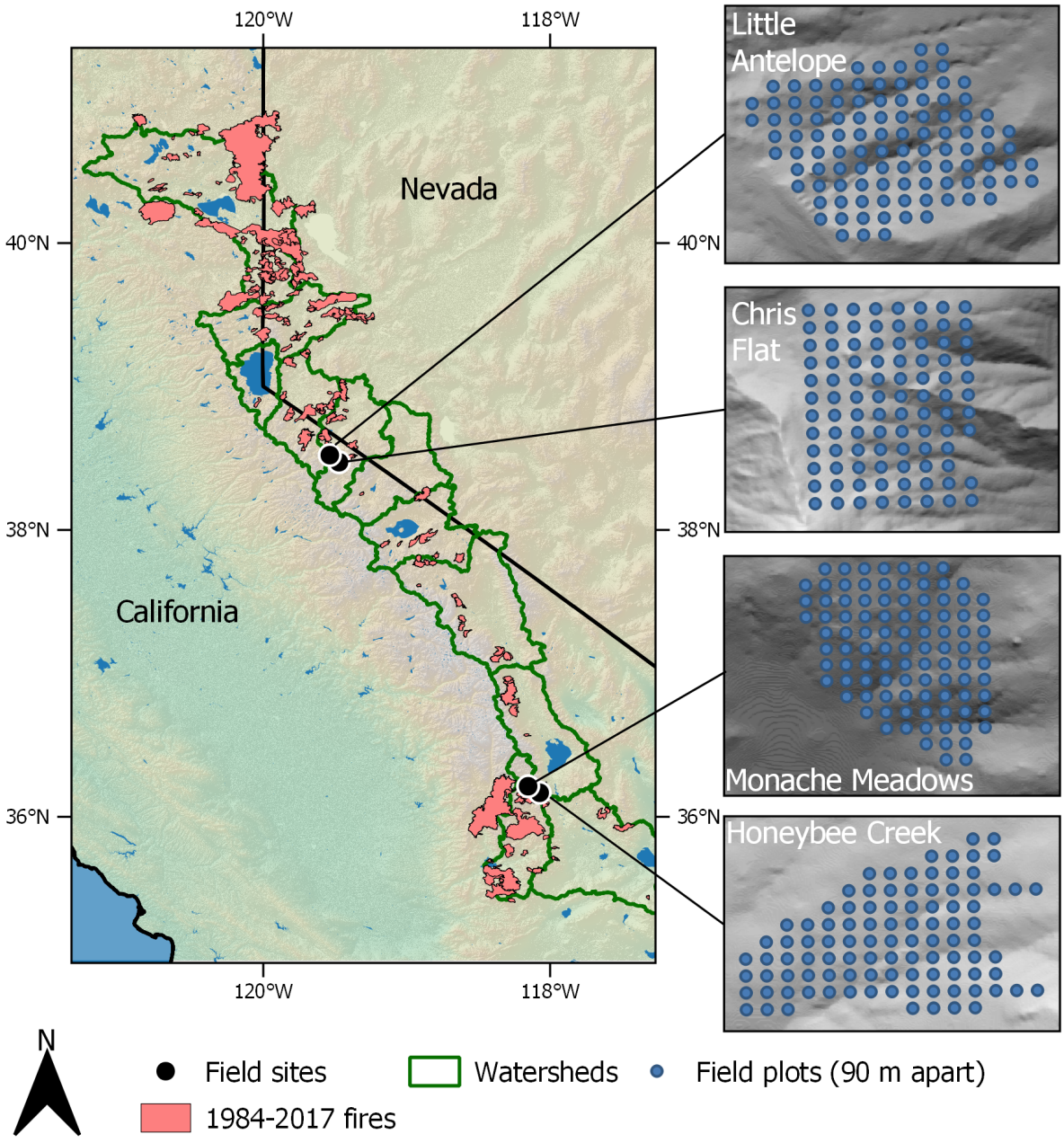


Fig. 1. Location of the four study sites in the eastern Sierra Nevada, California, USA, and the layout of field plots at each site. Green lines represent the 4th-level watersheds (Seaber et al. 1987) delineating the eastern side of the mountains.

dominant shrub variable. If shrub cover was not dominated by one of the five most common genera it was grouped into an "other" category.

We assessed the likely pre-fire presence/absence of individual tree species by counting a species present if a live or standing dead stem >5 cm dbh was found in the plot or if a non-decomposed log >7.6 cm diameter of that species was found intersecting one of the litter depth transects (i.e., Brown 1974). Plots in which trees

Table 1. Characteristics of the four study sites: latitude and longitude, number of plots surveyed (*n*), range and mean of plot elevations, the year of burn, and a breakdown of fire severity classes (in percentage of plots, based on the Relative differenced Normalized Burn Ratio). For full site names, see Fig. 1.

						Fire severity (%)		
Name	Long. (°)	Lat. (°)	*n*	Elevation (m)	Year of burn	Low	Moderate	High
CF	−119.47	38.47	94	1952–2362 (2139)	2002	28	44	29
LA	−119.54	38.52	106	1865–2246 (2023)	2002	9	57	34
HC	−118.07	36.17	99	2562–2787 (2649)	2008	27	36	36
MM	−118.15	36.21	98	2426–2551 (2483)	2003	30	41	30

had been present pre-fire but all trees were dead trees in 2017 were classified as stand-replacing fire plots. To quantify potential range shifts, we also grouped plots into the following categories for each species: tree loss and recovery if a species was present pre-fire but not post-fire, and regeneration of that species was absent or present respectively; and expansion if a seedling or sapling was present for a species that was not previously found in the plot.

Fire severity

Fire severity was quantified using the Relative differenced Normalized Burn Ratio (RdNBR, Miller and Thode 2007), an index of fire severity derived from Landsat TM data and available through the Monitoring Trends in Burn Severity (MTBS) program (Eidenshink et al. 2007). Relativizing dNBR to pre-fire values helps to correct for differences among areas with different vegetation types and canopy cover (Miller and Thode 2007), making the RdNBR more appropriate than dNBR for areas of heterogenous vegetation types and structures. We used continuous RdNBR values for statistical analysis but also report classified RdNBR (unchanged-low, moderate, and high severity) using type thresholds identified for fires throughout the Sierra Nevada (Miller and Thode 2007). Because MTBS provided RdNBR based on imagery from immediately following the 2002 Cannon Fire, we re-calculated RdNBR using one-year post-fire imagery for this fire to match the other fires (see Appendix S2 for details).

Terrain and water balance

We evaluated the influence of terrain and moisture on the presence or absence of tree regeneration using topographic and water balance indices. Topographic variables were calculated from a 10-m resolution digital elevation model and included slope pitch and Beers transformed aspect (Beers et al. 1966), where 0 represents southwestern exposure and 2 represents northeastern exposure. Topographic position index (TPI), an index of how high or low a pixel is relative to the elevation of surrounding pixels, was calculated using a 400-m neighborhood to represent localized valleys and ridges within the sites. Because sites had similar vegetation transitions but over different elevational ranges (Table 1), we subtracted the site-level median elevation of plots containing Jeffrey pine from raw elevation to create a standardized elevation variable that corrects for the elevation of the Jeffrey pine belt at each site.

To quantify spatial and temporal variation in water balance, we used AET and CWD data estimated using the California Basin Characterization Model (CBCM; Flint et al. 2013). The CBCM provided water balance metrics at 270 m resolution based on gridded climate data, terrain and soil properties, and simulated snowpack dynamics (Flint et al. 2013). Mean annual CWD and AET were temporally averaged for the water year (i.e., prior October–September) following a fire through 2016 to evaluate their influence on post-fire conditions.

Analysis

The primary goal of our statistical analysis was to characterize drivers of tree regeneration across a gradient of fire severity and to identity similarities and differences in regeneration among tree species. To accomplish this goal, we developed five statistical models of the presence

or absence of tree regeneration using random forest (RF; Breiman 2001): for all species combined, Jeffrey pine, pinyon pine, mountain mahogany, and all species in plots of stand-replacing fire. RF is a machine learning method that performs well when data are autocorrelated, when variables are interacting, and when relationships between response and predictor variables are non-linear (Cutler et al. 2007, Evans and Cushman 2009). Consequently, RF is well-suited for identifying the influence of multiple factors on tree regeneration in complex terrain. Based on prior knowledge (Appendix S1: Table S1), 17 variables were selected for analysis, that measured aspects of terrain, water balance, ground cover, understory vegetation, and tree species composition (Appendix S1: Table S2). A site variable was also included to account for unexplained among-site differences.

For each model, tree regeneration was more often absent than present. To prevent overprediction of the majority class, we used a balanced random forest with bootstrap samples drawn from each class such that class sizes are equal when growing each classification tree (Chen et al. 2004). Each RF model was grown using 2000 trees and three variables considered for splitting at each node. We evaluated the influence of spatial autocorrelation within each model and determined that it was unlikely to strongly affect our results (Appendix S3). To quantify variable importance such that results were comparable across models we used the Model Improvement Ratio (Murphy et al. 2010) normalized to the standard error of the importance values, as calculated in the rfUtilities R package (Evans and Murphy 2018). These variable importance values sum to one within each model with higher values indicating greater proportional importance.

Final model accuracy is reported as the out-of-bag percentage correctly classified (PCC), or the PCC calculated from the data not included in the bootstrap sample used to grow each tree (Breiman 2001, Liaw and Wiener 2002). Percentage of presence votes from the classification trees in each RF model were used as an estimate of the probability of tree regeneration (denoted as "predicted probability"), and maps of these probabilities were created as an additional assessment of model accuracy (Appendix S1: Figs. S2, S3). To show the relationships between individual variables and tree regeneration we used partial dependence plots generated with the pdp package in R (Greenwell 2017).

Future tree regeneration projections

To explore how climate change might affect post-fire tree regeneration by the end of the century, we used 2070–2099 water balance projections from the 2014 California Basin Characterization Model (Flint et al. 2013). This dataset provided AET and CWD estimates from nine global climate models (Flint et al. 2013) from the fifth phase of the Climate Model Intercomparison Project (Taylor et al. 2012). We used the statistical models to predict probability of tree regeneration (i.e., proportion of present votes from all classification trees) under these future water balance scenarios and compared them with probability under current post-fire water balance.

Results

Tree regeneration was absent at 50% of study plots across the four sites (Fig. 2). Previously forested plots (i.e., those with at least one tree pre-fire) had a mean density of 290 trees/ha pre-fire (median = 191 trees/ha) while the mean density of post-fire tree regeneration in forested plots was 152 trees/ha (median = 57 trees/ha). Jeffrey pine, pinyon pine, and mountain mahogany all had similar seedling and sapling density distributions (Fig. 2). Tree loss plots (Fig. 3) were more common than tree recovery plots and tree expansion plots for each species and overall. Pinyon pine, which was the least abundant of the three major tree species, had the most tree expansion plots (7.1% of all plots, Fig. 3).

The statistical models of tree regeneration ranged in accuracy from 68 to 80% correctly classified (Table 2). Five variables had particularly consistent and strong influences on tree regeneration, based on an importance ranking (Fig. 4) and partial dependence plots (Fig. 5). (1) AET had a strong positive influence on all species except mountain mahogany (Fig. 5). (2) Live basal area of conspecific tree species had a strong unimodal relationship with tree regeneration in four models, including sharp increases in tree regeneration likelihood from 0 to 5 m^2/ha and

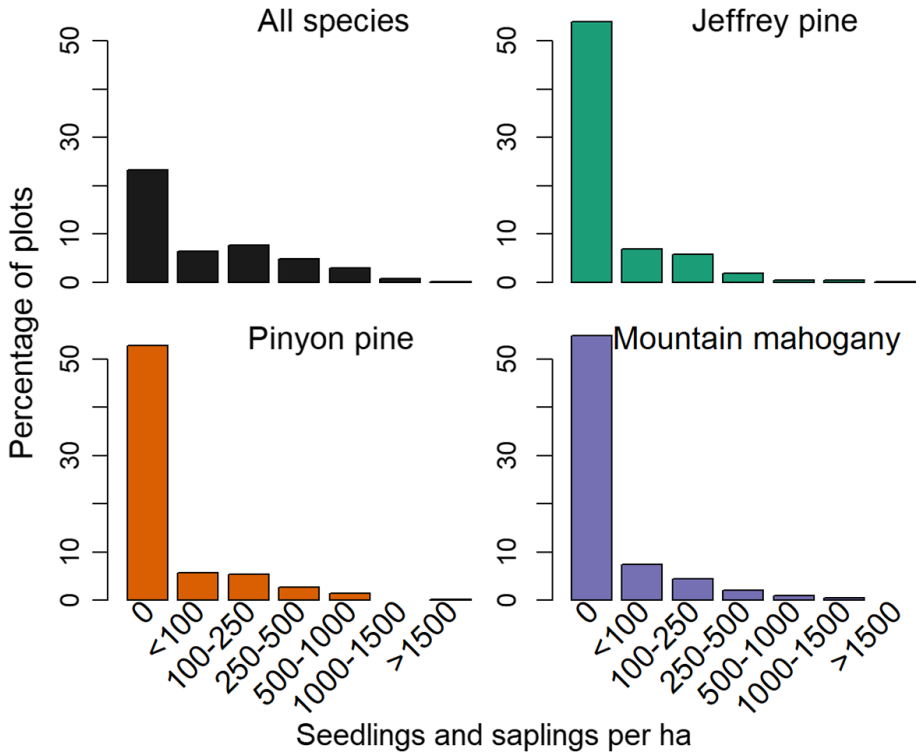


Fig. 2. The distribution of combined tree seedling and sapling density for all species and the three most abundant species, shown by percentage of all study plots (n = 397).

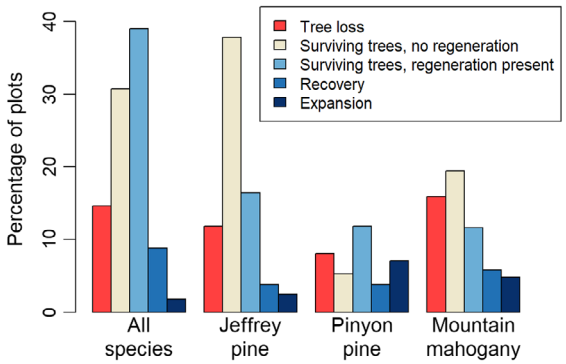


Fig. 3. Percentage of study plots with different combinations of tree presence/absence and regeneration presence/absence for all tree species combined as well as individual tree species.

declines beyond 20 m^2/ha. (3) Regeneration was more likely in plots dominated by *Artemesia* or *Ceanothus* shrubs in three models. (4) Slopes of 20°–35° were most likely to contain tree regeneration in three models. (5) Finally, fire severity as quantified by RdNBR had strong negative relationships with tree regeneration in the pinyon pine and stand-replacing fire models (Fig. 5). Despite the consistently strong and positive influence of AET, CWD had only low-moderate influence (Fig. 4) and its relationship with tree regeneration varied among species from negative (Jeffrey pine) to unimodal (pinyon pine) to positive (mountain mahogany; Fig. 6).

Surprisingly, based on 2070–2099 water balance scenarios, the likelihood of tree regeneration will increase in areas where tree regeneration is unlikely at present, and decrease in areas with currently high likelihood of regeneration (Fig. 7). Note that the bimodal distribution of current regeneration probability in Fig. 7, especially in the all species model, did not closely match any one variable such as site and instead reflected a tendency of the model to produce either low or high probabilities (see discussion in Appendix S4). The relationships between present and future likelihood of tree regeneration were highly similar across species and indicated a

Table 2. Confusion matrices showing number of plots correctly and incorrectly classified by random forest models of presence and absence of tree regeneration.

Model	Predicted	Present	Absent	Within-class PCC (%)
All species (70.6%)	Present	136	59	69.7
	Absent	57	143	71.5
Jeffrey pine (75.7%)	Present	57	33	63.3
	Absent	60	241	80.1
Pinyon pine (80.3%)	Present	75	14	84.3
	Absent	64	242	79.1
Mountain mahogany (68.4%)	Present	50	37	57.5
	Absent	88	220	71.4
Stand-replacing (73.1%)	Present	26	9	74.3
	Absent	16	42	72.4

Note: Overall percentage correctly classified (PCC) from out-of-bag samples is shown in parentheses, and within-class PCC is given in the right column.

future decrease in variability of potential for regeneration across the sites (Fig. 7). Regeneration likelihood tended to increase in areas with lower post-fire AET and decrease in areas with higher post-fire AET (Fig. 7).

Discussion

Fire and forest loss

The ability of fire to catalyze forest loss at low-elevation forest margins is a major challenge to maintaining semi-arid forest cover, especially as the climate warms (Parks et al. 2019, Davis et al. 2019*a*). The absence of tree regeneration in half of our plots suggests that fire may indeed be acting as a catalyst of forest loss across portions of the study site. Tree regeneration was also roughly 50% absent in studies of dry pine and mixed-conifer forest on the western side of the Sierra Nevada and the eastern side of the Rocky Mountains, which has a strong rain-shadow effect analogous to the ESN (Rother and Veblen 2016, Welch et al. 2016). Sparse or absent post-fire tree regeneration has also been widely noted in other semi-arid pine forests, especially close to the lower treeline or in high-severity burn patches (Donato et al. 2016, Owen et al. 2017, Haffey et al. 2018, Stoddard et al. 2018, Coop et al. 2019, Kemp et al. 2019). Similarly, tree regeneration in pinyon–juniper woodlands may take decades to over a century to occur following high-severity fire, especially if shrubs that act as nurse plants are killed (Erdman 1970, Koniak 1985, Romme et al. 2009). Although low-elevation forest margins are typically low-density stands with highly episodic recruitment (Savage et al. 1996, League and Veblen 2006), absence of post-fire tree regeneration is still suggestive of forest loss and begs the question of where on the landscape these losses might occur.

Community reshuffling

Fires may catalyze not just forest loss, but also compositional shifts in tree species. The distributions of tree regeneration densities were markedly similar for Jeffrey pine, pinyon pine, and mountain mahogany. Crucially, though, Jeffrey pine had been present in 70% of plots pre-fire whereas pinyon pine and mountain mahogany had only been present in 29% and 53% of plots respectively. Furthermore, pinyon pine regeneration had expanded into 28 plots (7.1%) in which the species had been absent pre-fire, compared with 19 such plots for mountain mahogany and 10 for Jeffrey pine. Therefore, the fires appear to have shifted species composition toward mountain mahogany and especially pinyon pine. Pinyon pine may have a particular advantage dispersing into burned areas because its seeds are extensively transported and cached by corvids (jays and nutcrackers) and rodents, who by burying seeds facilitate seedling emergence (Vander Wall and Balda 1981, Chambers 2001, Hollander and Vander Wall 2004). However, secondary dispersal by birds and rodents has also been observed for Jeffrey pine and western juniper and is therefore not unique to pinyon pine at our sites (Vander Wall 2008, Briggs et al. 2009, Dimitri and Longland 2017).

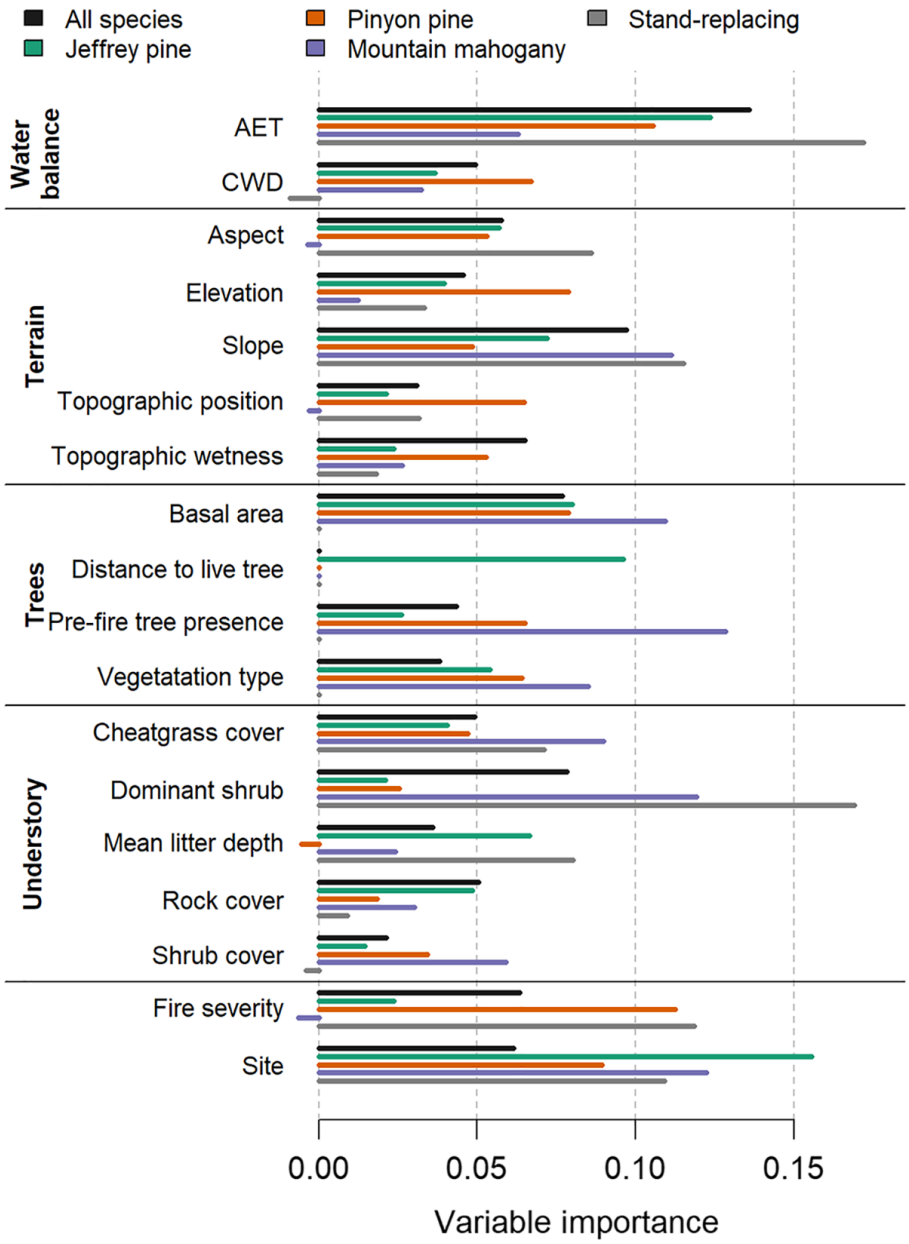


Fig. 4. Scaled variable importance for the models of tree regeneration (colored lines). Variables are grouped into categories (bolded text). AET is actual evapotranspiration, and CWD is climatic water deficit.

In a warming climate and given a lack of frequent fire, upslope expansion of drought-tolerant species like pinyon pine and mountain mahogany into Jeffrey pine forest in the ESN may become increasingly likely. In California's Santa Rosa Mountains, climate change has been implicated in an upslope shift of the Jeffrey pine-oak woodland ecotone (Kelly and Goulden 2008). Similarly, regeneration failure of ponderosa pine at the ecotone with pinyon–juniper woodland in Arizona suggests upslope retreat of ponderosa pine and upslope migration of pinyon–juniper woodland (Minott and Kolb 2020). Expansion of drought-tolerant woodland tree species at forest-

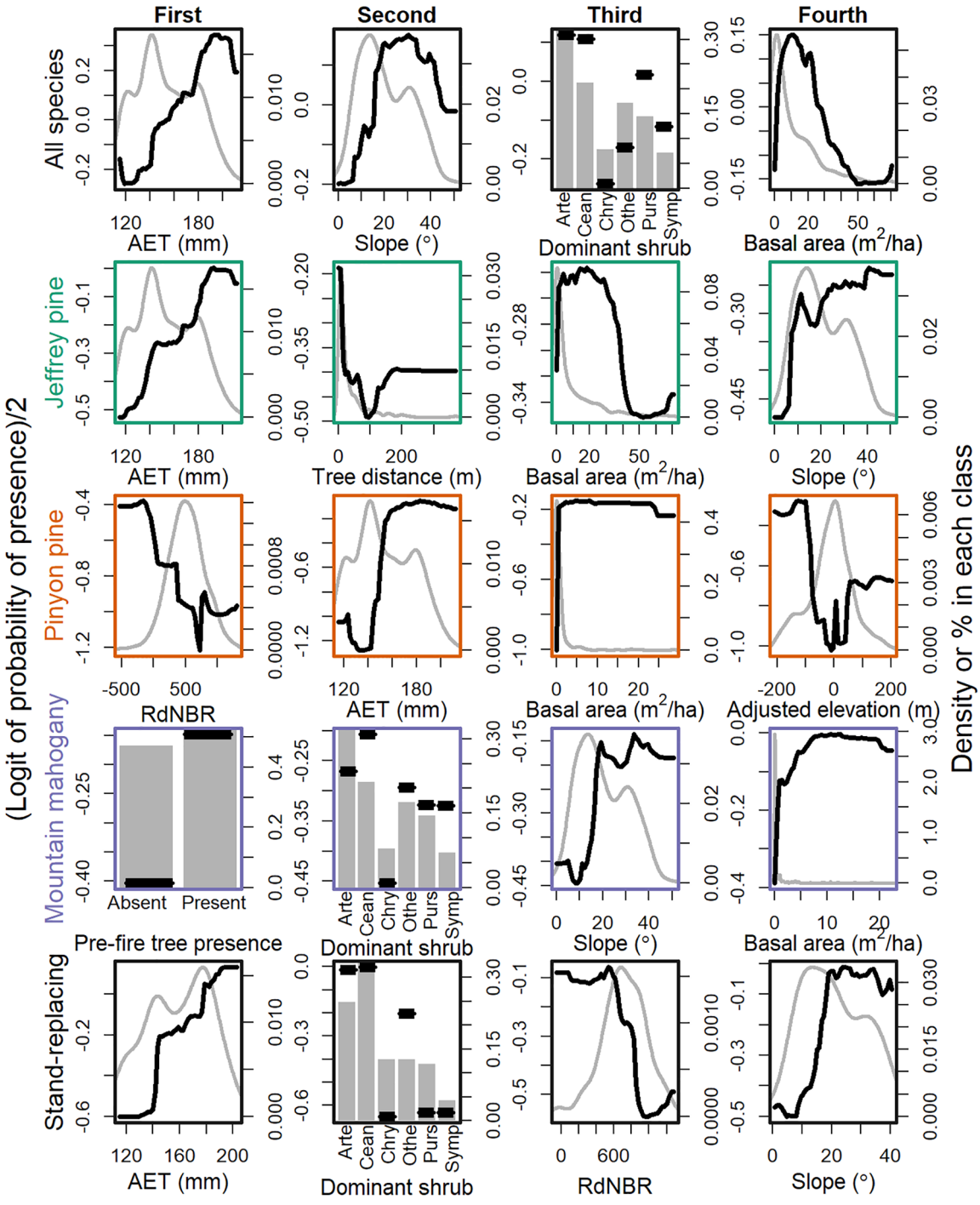


Fig. 5. Partial dependence plots showing the relationship between individual variables and the probability of tree regeneration being present. Each row displays the top four variables for a different model, labeled at left and color-coded (see Table 2 for model accuracy). The gray lines and bars display the distribution of each variable using either a density plot (quantitative variables) or the percentage in each class (qualitative variables). AET, actual evapotranspiration; TWI, topographic wetness index; RdNBR, Relative differenced Normalized Burn Ratio; Arte, *Artemesia*; Cean, *Ceanothus*; Chyr, *Chrysothamnus*; Othe, othef; Purs, *Purshia*; Symp, *Symphoricarpos*.

steppe ecotones therefore appears to be a widespread phenomenon in the southwestern United States, and analogous shifts toward more drought-tolerant but less fire-tolerant species at other low-elevation forest margins deserve further attention.

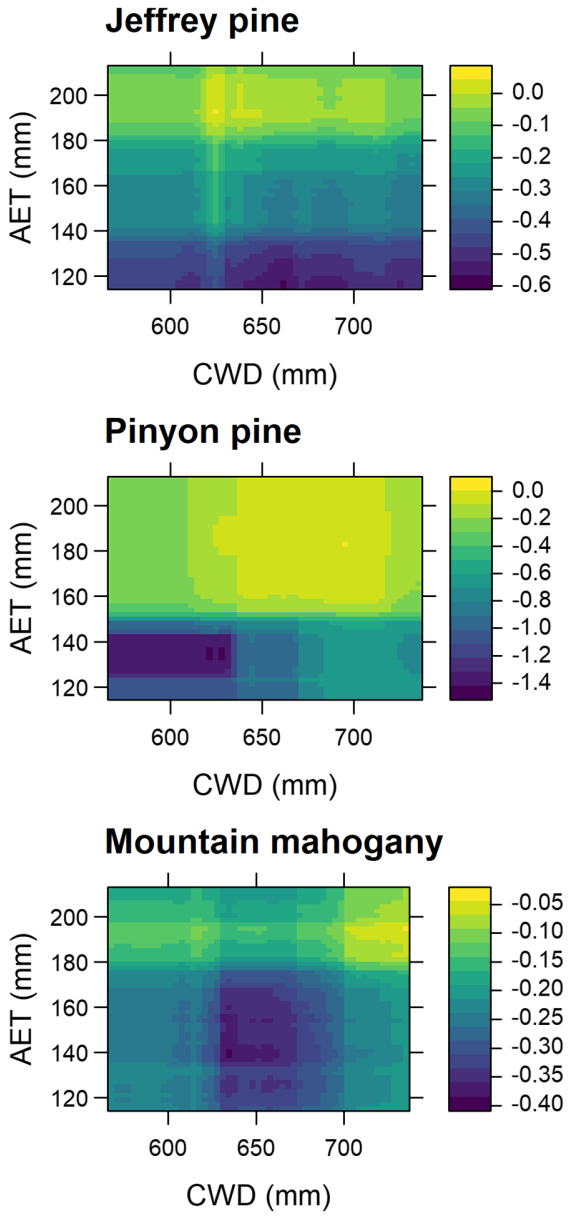


Fig. 6. Influence of climatic water deficit (CWD) and actual evapotranspiration (AET) on the probability of tree regeneration being present for different species, as shown using partial dependence plots. Yellow (blue) colors indicate higher (lower) probability of tree regeneration.

Another notable difference among species was how they responded to local vegetation and ground cover. Mountain mahogany was less sensitive to topoclimate probably because it tends to grow on rocky and poor soils, which may reflect a capacity to fix its own nitrogen from nitrogen-fixing root nodules (Lepper and Fleschner 1977, Davis and Brotherson 1991). Consequently, mountain mahogany's range may be more strongly constrained by substrate than the other tree species. Mountain mahogany seeds also rely primarily on wind dispersal, in contrast to the other species which often experience secondary dispersal by birds and rodents (Russell and Schupp 1998, Hollander and Vander Wall 2004, Briggs et al. 2009). This dispersal limitation could also factor into the stronger influence of local vegetation for mountain mahogany regeneration, in particular the presence of conspecific trees within plots.

Vegetation and fire severity

Patterns of surviving trees, as determined by fire severity, strongly influence post-fire tree regeneration of obligate seeders by governing seed source (Coop et al. 2019, Downing et al. 2019). Additionally, areas shaded by a tree canopy typically experience lower daytime temperatures and have higher surface soil moisture, likely facilitating tree regeneration in stressful environments (Chen et al. 1999, Davis et al. 2019*b*). The effects of canopy cover on soil moisture are notably complex; Breshears et al. (2009) found that areas under the tree canopy in a pinyon–juniper woodland had more consistent water availability than inter-canopy areas in shallow soils (<20 cm) and bedrock, but not in deeper soils in between. Thin soils underlain by weathered bedrock are typical of California forests, and trees may rely extensively on bedrock water once soil water is depleted in late spring or early summer (Hubbert et al. 2001). Yellow pine seedlings in the Sierra Nevada commonly access bedrock water within only 2–3 yr of establishment, suggesting that sparsely studied bedrock water dynamics may be crucial to understanding seedling growth and mortality (Witty et al. 2003, Breshears et al. 2009). The positive relationship we observed between live tree basal area and tree

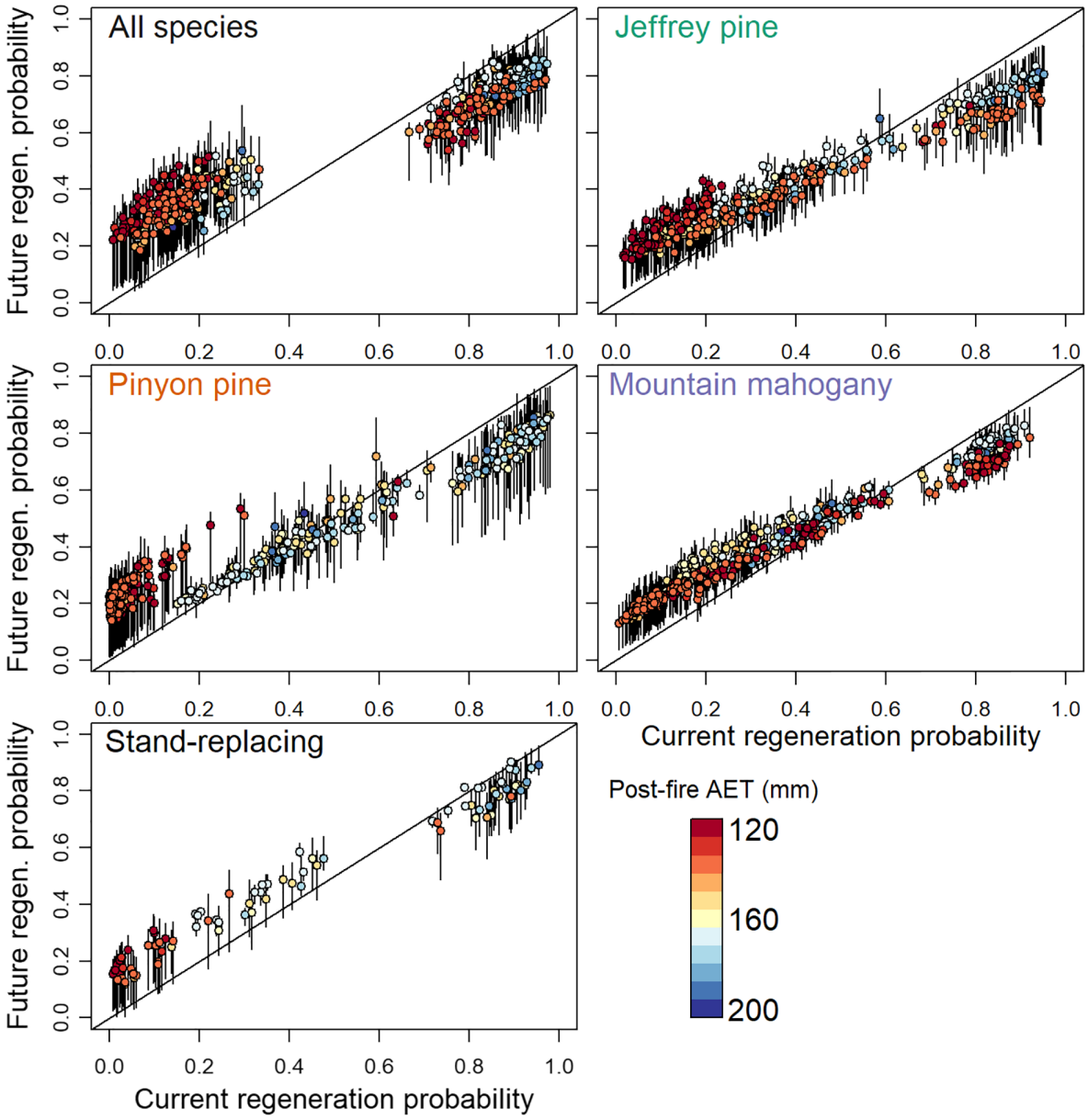


Fig. 7. Predicted probability that tree regeneration is present in each field plot according to each model using post-fire water balance (*x*-axis) versus projected 2070–2099 mean water balance (*y*-axis). Lines and points show the range and mean probability of regeneration based on 11 future climate scenarios. The black line represents equal probability of regeneration under post-fire and future conditions. Colors represent post-fire actual evapotranspiration (AET).

regeneration up to ~20–30 m^2 ha^{-1} is likely due to a combination of seed source and microclimatic effects whereas the strong influence of distance to the nearest Jeffrey pine tree on Jeffrey pine regeneration reflects seed source limitations in high-severity fire patches.

At the scale of an individual seedling within our sites, vegetation and ground cover may better explain gradients of water balance than terrain-driven variability. For example, maximum daily growing season air temperatures at 10 cm above the ground are 5.3°C lower in the forest

than in adjacent open areas in western U.S. forests (Davis et al. 2019*b*). The temperature lapse rate in the ESN is about 8.6°C per 1 km elevation (Potter 1998), which suggests that a seedling growing among surviving trees may experience maximum temperatures equivalent to a seedling growing in the open but 600 m higher in elevation. For comparison, our maximum within-site elevation range is 410 m (Table 1). These rough calculations suggest that the influence of tree cover on microclimate substantially moderates and may even outweigh the influence of terrain at our scale of analysis (i.e., ~1 km^2 extent).

Litter cover additionally moderates soil temperature and moisture and therefore contributes to successful tree regeneration (Bonnet et al. 2005). The positive relationships between litter cover and tree regeneration in our models (Appendix S1: Table S1), which were especially important in areas of stand-replacing fire, is consistent with this further influence of litter on microclimate. Shrubs may further moderate soil moisture and temperature and sometimes provide additional nutrients, which means that shrub cover may be crucial to tree regeneration especially in arid environments (Chambers 2001, Legras et al. 2010, Alpert and Loik 2013, Ziffer-Berger et al. 2014). Therefore, the areas of highest drought intensity and lowest moisture availability at our scale of analysis may not necessarily be those in the hottest and driest topographic settings, but rather areas of unshaded bare soil. Combining the mesoscale influence of topoclimate with the microscale influence of vegetation and ground cover would improve predictions of tree regeneration and represents a potential avenue of future research.

Although cheatgrass cover had only a moderate direct influence on tree regeneration, cheatgrass was abundant at lower-elevation and more xeric landscape positions at the two northern sites (Appendix S1: Fig. S4). Fire-initiated transitions to non-forest can be reinforced over time by cheatgrass, because fire risk increases with cheatgrass cover and successive fires increase cheatgrass dominance at the expense of woody plant cover (Link et al. 2006, Davies et al. 2012, Bradley et al. 2018). Cheatgrass is patchily distributed throughout the ESN but is likely to become more abundant and expand upslope as the climate warms, and fire may facilitate this expansion by reducing competition from trees and understory plants (Crawford et al. 2001, Gundale et al. 2008, Concilio et al. 2013, Peeler and Smithwick 2018).

Water balance

Increased water deficit since the turn of the century has been linked to decreases in tree regeneration in the U.S. Rocky Mountains (Stevens-Rumann et al. 2018), and research in the southern Rocky Mountains found that both AET and CWD were critical determinants of successful regeneration (Rodman et al. 2019). Although we expected both AET and CWD to strongly influence tree regeneration, only AET had a strong and consistent influence on tree regeneration across our analyses. High CWD was only linked to low likelihood of tree regeneration for Jeffrey pine, which is also supported by experimental work that shows drought intensity limits ponderosa and Jeffrey pine seedling survival (Legras et al. 2010, Alpert and Loik 2013, Simeone et al. 2019). For pinyon pine and mountain mahogany, intermediate–high CWD actually corresponded with greater probability of tree regeneration. Notably, CWD was unrelated to *Pinus edulis* regeneration in the southwestern United States and post-disturbance recruitment depended instead on nurse trees and shrubs (Redmond et al. 2015). However, Minott and Kolb (2020) found that *Pinus edulis* regeneration was positively related to mean annual precipitation, which is consistent with the positive relationship we observed between pinyon pine regeneration and AET. Similarly, the weak response of pinyon pine and mountain mahogany to CWD and the strong response to tree cover and fire severity in our study suggest that nurse plants and AET but not mesoscale water deficit are key to understanding post-disturbance woodland recovery in the ESN.

Because projections indicate that both AET and CWD will increase by the end of the century in the ESN, we did not find evidence of an upslope shift in the potential for tree regeneration. Instead, variability in tree regeneration within sites actually decreased including a trend toward greater likelihood of regeneration at the driest portions of the sites and a trend toward decreasing likelihood in the most mesic locations. The explanation for these projections within the scope of our statistical model is that, at the driest

portion of the sites, projected increases in AET led to a greater likelihood of tree regeneration and outweighed the effects of projected increases in CWD. By contrast, the more mesic portions of the sites already had sufficient AET to support tree regeneration and therefore did not benefit from further increases, but increases in CWD led to slightly lower likelihood of tree regeneration. These surprising projections do not fit the prevailing view that increasing water deficit will lead to upslope shifts in tree regeneration and regeneration failure at lower forest margins (Davis et al. 2019*a*). Under that narrative, high-severity disturbance accelerates climate-driven trends toward upslope forest retreat (Stevens-Rumann et al. 2018, Kemp et al. 2019). Given a strong directional influence of climate change on tree regeneration, triggering a switch to a non-forested state becomes increasingly likely and eventually inevitable (Johnstone et al. 2016). However, for regions in which AET is increasing, vegetation switching may not be inevitable and high-severity disturbance may be a prerequisite for upslope forest retreat. In such regions, trailing-edge forests may actually be resilient to climate change so long as high-severity disturbance can be avoided.

We observed little recent tree mortality (i.e., dead trees with needles or fine branches) at our sites in the ESN in 2017 despite a severe and long-duration drought in California from 2012 to 2015 which caused widespread tree mortality on the western side of the Sierra Nevada along with pockets of high mortality on the eastern side (Young et al. 2017). Therefore, forests at these sites may be resistant to severe multi-year droughts, which are becoming increasingly likely in California (Swain et al. 2016). Because denser stands tended to experience greater mortality from the drought and associated bark beetle outbreaks in the Sierra Nevada (Fettig et al. 2019, Restaino et al. 2019), low tree density may have contributed to drought resistance at our sites (127 ± 233 live trees/ha in 2017 vs. 397 ± 292 trees/ha in pine and mixed-conifer forests throughout the Sierra Nevada; Safford and Stevens 2017). However, lack of post-fire tree regeneration at our sites where fire killed most trees suggests forest loss may occur with high-severity fire. Across the ESN, 18.5% of yellow pine forests were burned between 1984 and 2017 and 48% was high-severity fire, and 14.4% of pinyon–juniper woodland burned and 54% was high-severity fire (Harris 2019). The high percentage of high-severity fire in recent fires suggests that fire is generating substantial forest loss and vegetation switching in locations where forests might otherwise be resilient.

The extent to which low-elevation forest margins may be resilient to climate change but highly vulnerable to high-severity disturbance is largely unknown and deserves further research. As temperatures continue to rise, evaporative demand and drought intensity will increase and consequently increased tree mortality from drought, insect outbreaks and wildfire may drive forest retreat (Williams et al. 2013). California may be unusual since mean annual precipitation is projected to increase in the northern and central portions of the state, which may moderate increases in drought intensity and lead to greater AET (Polade et al. 2017, Pierce et al. 2018, Swain et al. 2018). However, Petrie et al. (2017) used future water balance projections to predict regeneration potential for ponderosa pine and found that potential will increase during the next four decades in the U.S. Intermountain West before declining at the end of the century due to increased seedling mortality from continued warming. The regeneration projections for ponderosa pine suggest that climate change may not uniformly reduce tree regeneration in all locations and time periods. Especially in other rain-shadow locations in which trees are highly drought-tolerant, forests may persist in a changing climate unless tree cover is removed through high-severity disturbance.

Conclusion

The absence of tree regeneration in half of our field plots and the low seedling densities in other plots, including many burned at high severity, suggest that wildfire could cause lasting loss of tree cover. The fires may have also generated a shift toward drought-tolerant but fire-sensitive species. Because tree regeneration had a strong positive response to AET and because AET is projected to increase in the future at these sites, we do not find evidence of climate-driven upslope retreat of forests. In the absence of strong directional effects of climate change on tree regeneration, these sites may be resilient to climate change and low-severity disturbances. In

areas where forest cover survives wildfire, tree regeneration may be more robust and fuels will be reduced. The result will be an area that is more resilient to future warming. On the other hand, high-severity fire removes cover of trees and nurse shrubs which are important to tree regeneration and amelioration of local drought stress, causing a transition to non-forest that may be difficult to reverse. Consequently, patterns of fire severity may determine the future mosaic of semi-arid forest and non-forest in this and other rain-shadow landscapes, and avoiding high-severity fire may be critical to long-term maintenance of tree cover.

Acknowledgments

We thank John Campbell, Natalie Pawlikowski, Anthony Zhao, and Joe Breznicky for conducting fieldwork; Marc Meyer and Duncan Leao for advice and logistical support; Andrew Carleton, Laura Leites, and Erica Smithwick for their comments on earlier versions of the manuscript; and two anonymous reviewers for their valuable comments. This project was funded by a NSF Doctoral Dissertation Research Improvement Award (No. 1735558) and by a Center for Landscape Dynamics research award and a Ruby S. Miller Graduate Student Fellowship from The Pennsylvania State University.

Literature Cited

Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest – woodland ecotone: rapid landscape response response to climate variation. Proceedings of the National Academy of Sciences 95:14839–14842.

Alpert, H., and M. E. Loik. 2013. *Pinus jeffreyi* establishment along a forest-shrub ecotone in eastern California, USA. Journal of Arid Environments 90:12–21.

Ashcroft, M. B., J. R. Gollan, D. I. Warton, and D. Ramp. 2012. A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. Global Change Biology 18:1866–1879.

Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. Journal of Forestry 64:691–692.

Bonnet, V. H., A. W. Schoettle, and W. D. Shepperd. 2005. Postfire environmental conditions influence the spatial pattern of regeneration for *Pinus ponderosa*. Canadian Journal of Forest Research 35:37–47.

Bradley, B. A., C. A. Curtis, E. J. Fusco, J. T. Abatzoglou, J. K. Balch, S. Dadashi, and M. N. Tuanmu. 2018. Cheatgrass (*Bromus tectorum*) distribution in the intermountain Western United States and its relationship to fire frequency, seasonality, and ignitions. Biological Invasions 20:1493–1506.

Breiman, L. 2001. Random forests. Machine Learning 45:5–32.

Breshears, D. D., O. B. Myers, and F. J. Barnes. 2009. Horizontal heterogeneity in the frequency of plant-available water with woodland intercanopy-canopy vegetation patch type rivals that occuring vertically by soil depth. Ecohydrology 2:503–519.

Briggs, J. S., S. B. Vander Wall, and S. H. Jenkins. 2009. Forest rodents provide directed dispersal of Jeffrey pine seeds. Ecology 90:675–687.

Brooks, M. L., C. S. Brown, J. C. Chambers, C. M. D'Antonio, J. E. Keeley, and J. Belnap. 2016. Exotic annual Bromus invasions: comparisons among species and ecoregions in the western United States. Pages 11–60 *in* M. J. Germino, J. C. Chambers and C. S. Brown, editors. Exotic brome-grasses in arid and semiarid ecosystems of the Western US. Springer International Publishing, Cham, Switzerland.

Brown, J. 1974. Handbook for inventorying downed woody material. GTR-INT-16. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.

Brown, P., and R. Wu. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. Ecology 86:3030–3038.

Burwell, T. 1998. Successional patterns of the lower montane treeline, eastern California. Madrono 45:12–16.

Chambers, J. C. 2001. Pinus monophylla establishment in an expanding *Pinus-Juniperus* woodland: environmental conditions, facilitation and interacting factors. Journal of Vegetation Science 12:27–40.

Chambers, M. E., P. J. Fornwalt, S. L. Malone, and M. A. Battaglia. 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine - dominated forests of the Colorado Front Range. Forest Ecology and Management 378:57–67.

Chen, C., A. Liaw, and L. Breiman. 2004. Using random forest to learn imbalanced data. Technical Report 666. Statistics Department, University of California, Berkeley, California, USA.

Chen, J., et al. 1999. Microclimate in forest ecosystem and landscape ecology. BioScience 49:288–297.

Concilio, A. L., M. E. Loik, and J. Belnap. 2013. Global change effects on *Bromus tectorum* L. (Poaceae) at its high-elevation range margin. Global Change Biology 19:161–172.

Coop, J. D., T. J. Delory, W. M. Downing, S. L. Haire, M. A. Krawchuk, C. Miller, M. A. Parisien, and R. B. Walker. 2019. Contributions of fire refugia to resilient ponderosa pine and dry mixed-conifer forest landscapes. Ecosphere 10. https://doi.org/10.1002/ecs2.2809

Crawford, J. A., C.-H.-A. Wahren, S. Kyle, and W. H. Moir. 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. Journal of Vegetation Science 12:261–268.

Cutler, D. R., T. C. Edwards, K. H. Beard, A. Cutler, K. T. Hess, J. Gibson, and J. J. Lawler. 2007. Random forests for classification in ecology. Ecology 88:2783–2792.

Davies, G. M., J. D. Bakker, E. Dettweiler-Robinson, P. W. Dunwiddie, S. A. Hall, J. Downs, and J. Evans. 2012. Trajectories of change in sagebrush steppe vegetation communities in relation to multiple wildfires. Ecological Applications 22:1562–1577.

Davis, F. W., et al. 2016. Shrinking windows of opportunity for oak seedling establishment in southern California mountains. Ecosphere 7:1–18.

Davis, J. N., and J. D. Brotherson. 1991. Ecological relationships of curlleaf mountain-mahogany (*Cercocarpus ledifolius* Nutt.) communities in Utah (USA) and implications for management. Great Basin Naturalist 51:153–166.

Davis, K. T., S. Z. Dobrowski, P. E. Higuera, Z. A. Holden, T. T. Veblen, M. T. Rother, S. A. Parks, A. Sala, and M. Maneta. 2019*a*. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proceedings of the National Academy of Sciences 116:6193–6198.

Davis, K. T., S. Z. Dobrowski, Z. A. Holden, P. E. Higuera, and J. T. Abatzoglou. 2019*b*. Microclimatic buffering in forests of the future: the role of local water balance. Ecography 42:1–11.

Dimitri, L. A., and W. S. Longland. 2017. Distribution of western juniper seeds across an ecotone and implications for dispersal. Western North American Naturalist 77:212–222.

Dobrowski, S. Z., A. K. Swanson, J. T. Abatzoglou, Z. A. Holden, H. D. Safford, M. K. Schwartz, and D. G. Gavin. 2015. Forest structure and species traits mediate projected recruitment declines in western US tree species. Global Ecology and Biogeography 24:917–927.

Donato, D. C., B. J. Harvey, and M. G. Turner. 2016. Regeneration of montane forests 24 years after the 1988 Yellowstone fires : A fire-catalyzed shift in lower treelines? Ecosphere 7:1–16.

Downing, W. M., M. A. Krawchuk, G. W. Meigs, S. L. Haire, J. D. Coop, R. B. Walker, E. Whitman, G. Chong, and C. Miller. 2019. Influence of fire refugia spatial pattern on post-fire forest recovery in Oregon's Blue Mountains. Landscape Ecology 34:771–792.

Eidenshink, J., B. Schwind, K. Brewer, Z. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. Fire Ecology 3:3–21.

Erdman, J. A. 1970. Pinyon-juniper succession after natural fires on residual soils of Mesa Verde, Colorado. Brigham Young University Science Bulletin, Biological Series 11:1–26.

Evans, J. S., and S. A. Cushman. 2009. Gradient modeling of conifer species using random forests. Landscape Ecology 24:673–683.

Evans, J. S., and M. A. Murphy. 2018. rfUtilities. R package version 2.1. https://cran.r-project.org/package=rfUtilities

Fettig, C. J., L. A. Mortenson, B. M. Bulaon, and P. B. Foulk. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. Forest Ecology and Management 432:164–178.

Flint, L. E., A. L. Flint, J. H. Thorne, and R. Boynton. 2013. Fine-scale hydrologic modeling for regional landscape applications: the California Basin Characterization Model development and performance. Ecological Processes 2:25.

Franklin, J., J. M. Serra-Diaz, A. D. Syphard, and H. M. Regan. 2016. Global change and terrestrial plant community dynamics. Proceedings of the National Academy of Sciences 113:3725–3734.

Geldenhuys, C. J. 1994. Bergwind fires and the location pattern of forest patches in the southern Cape landscape, South Africa. Journal of Biogeography 21:49–62.

Gill, L., and A. H. Taylor. 2009. Top-down and bottom-up controls on fire regimes along an elevational gradient on the east slope of the Sierra Nevada, California, USA. Fire Ecology 5:57–75.

Gómez-Aparicio, L., R. Zamora, J. M. Gómez, J. A. Hódar, J. Castro, and E. Baraza. 2004. Applying plant facilitation to forest restoration in Mediterranean ecosystems: a meta-analysis of the shrubs as nurse plants. Ecological Applications 14:1118–1138.

Greenwell, B. M. 2017. pdp: an R Package for Constructing Partial Dependence Plots. R Journal 9:1–16.

Gruell, G. 1999. Historical and Modern Roles of Fire in Pinyon-Juniper. Pages 24–28 *in* S. B. Monsen and R.

Stevens, editors. Proceedings: ecology and management of pinyon-juniper communities within the Interior West. RMRS-P-9, USDA Forest Service, Rocky Mountain Research Station. Ogden, Utah, USA.

Gundale, M. J., S. Sutherland, and T. H. DeLuca. 2008. Fire, native species, and soil resource interactions influence the spatio-temporal invasion pattern of Bromus tectorum. Ecography 31:201–210.

Haffey, C., T. D. Sisk, C. D. Allen, A. E. Thode, and E. Q. Margolis. 2018. Limits to ponderosa pine regeneration following large high-severity forest fires in the United States Southwest. Fire Ecology 14:143–163.

Harris, L. B. 2019. Fire-driven alternative states and spatial variability in forest resilience at a dry forest ecotone. The Pennsylvania State University, State College, Pennsylvania, USA.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Global Ecology and Biogeography 25:655–669.

Hollander, J. L., and S. B. Vander Wall. 2004. Effectiveness of six species of rodents as dispersers of singleleaf piñon pine (*Pinus monophylla*). Oecologia 138:57–65.

Hubbert, K. R., J. L. Beyers, and R. C. Graham. 2001. Roles of weathered bedrock and soil in seasonal water relations of *Pinus jeffreyi* and *Arctostaphylos patula*. Canadian Journal of Forest Research 31:1947–1957.

Ibáñez, I., and E. W. Schupp. 2002. Effects of litter, soil surface conditions, and microhabitat on *Cercocarpus ledifolius* Nutt. Seedling emergence and establishment. Journal of Arid Environments 52: 209–221.

Jackson, S. T., J. L. Betancourt, R. K. Booth, and S. T. Gray. 2009. Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. Proceedings of the National Academy of Sciences of the United States of America 106:19685–19692.

Johnstone, J. F., et al. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369–378.

Kelly, A., and M. Goulden. 2008. Rapid shifts in plant distribution with recent climate change. Proceedings of the National Academy of Sciences 105:11823–11826.

Kemp, K. B., P. E. Higuera, P. Morgan, and J. T. Abatzoglou. 2019. Climate will increasingly determine post-fire tree regeneration success in low-elevation forests, Northern Rockies, USA. Ecosphere 10:1–17.

Kersten, E. W. J. 1964. The early settlement of Aurora, Nevada, and nearby mining camps. Annals of the Association of American Geographers 54:490–507.

Kitchen, S. G. 2012. Historical fire regime and forest variability on two eastern Great Basin fire-sheds (USA). Forest Ecology and Management 285:53–66.

Koniak, S. 1985. Succession in pinyon-juniper woodlands following wildfire in the Great Basin. Great Basin Naturalist 45:556–566.

League, K., and T. T. Veblen. 2006. Climatic variability and episodic *Pinus ponderosa* establishment along the forest-grassland ecotones of Colorado. Forest Ecology and Management 228:98–107.

Legras, E. C., S. B. Vander Wall, and D. I. Board. 2010. The role of germination microsite in the establishment of sugar pine and Jeffrey pine seedlings. Forest Ecology and Management 260:806–813.

Lenoir, J., T. Hattab, and G. Pierre. 2017. Climatic microrefugia under anthropogenic climate change: implications for species redistribution. Ecography 40:253–266.

Lepper, M. G., and M. Fleschner. 1977. Nitrogen fixation by *Cercocarpus ledifolius* (Rosaceae) in pioneer habitats. Oecologia 27:333–338.

Liang, S., M. D. Hurteau, and A. L. R. Westerling. 2017. Response of Sierra Nevada forests to projected climate–wildfire interactions. Global Change Biology 23:2016–2030.

Liaw, A., and M. Wiener. 2002. Classification and Regression by randomForest. R News 2:18–22.

Link, S. O., C. W. Keeler, R. W. Hill, and E. Hagen. 2006. *Bromus tectorum* cover mapping and fire risk. International Journal of Wildland Fire 15:113–119.

Lutz, J. A., J. W. van Wagtendonk, and J. F. Franklin. 2010. Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. Journal of Biogeography 37:936–950.

McLaughlin, B. C., D. D. Ackerly, P. Z. Klos, J. Natali, T. E. Dawson, and S. E. Thompson. 2017. Hydrologic refugia, plants, and climate change. Global Change Biology 23:2941–2961.

Miller, A. D., J. R. Thompson, A. J. Tepley, and K. J. Anderson-Teixeira. 2018. Alternative stable equilibria and critical thresholds created by fire regimes and plant responses in a fire-prone community. Ecography 41:1–12.

Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sensing of Environment 109:66–80.

Miller, R. F., and R. J. Tausch. 2001. The role of fire in juniper and pinyon woodlands: a descriptive analysis. Pages 15–30 *in* K. E. M. Galley, and T. P. Wilson, editors. Proceedings of the Invasive Species

Workshop: the Role of Fire in the Control and Spread of Invasive Species. Fire Conference 2000: the First National Congress on Fire Ecology, Prevention and Management. Miscellaneous Publication No. 11, Tall Timbers Research Station, Tallahassee, Florida, USA.

Miller, R. F., R. J. Tausch, E. D. McArthur, D. D. Johnson, and S. C. Sanderson. 2008. Age structure and expansion of pinyon-juniper woodlands: a regional perspective in the Intermountain West. RMRS-RP-69, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Minott, J. A., and T. E. Kolb. 2020. Regeneration patterns reveal contraction of ponderosa forests and little upward migration of pinyon-juniper woodlands. Forest Ecology and Management 458: 117640.

Moody, T. J., J. Fites-Kaufman, and S. L. Stephens. 2006. Fire history and climate influences from forests in the northern Sierra Nevada, USA. Fire Ecology 2:115–127.

Murphy, M. A., J. S. Evans, and A. Storfer. 2010. Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. Ecology 91:252–261.

North, M. P., K. M. van de Water, S. L. Stephens, and B. M. Collins. 2009. Climate, rain shadow, and human-use influences on fire regimes in the Eastern Sierra Nevada, California, USA. Fire Ecology 5:20–34.

Owen, S. M., C. H. Sieg, A. J. Sánchez Meador, P. Z. Fulé, J. M. Iniguez, L. S. Baggett, P. J. Fornwalt, and M. A. Battaglia. 2017. Spatial patterns of ponderosa pine regeneration in high-severity burn patches. Forest Ecology and Management 405:134–149.

Parks, S. A., S. Z. Dobrowski, J. D. Shaw, and C. Miller. 2019. Living on the edge: trailing edge forests at risk of fire-facilitated conversion to non-forest. Ecosphere 10:e02651.

Peeler, J. L., and E. A. H. Smithwick. 2018. Exploring invasibility with species distribution modeling: How does fire promote cheatgrass (*Bromus tectorum*) invasion within lower montane forests? Diversity and Distributions 24:1308–1320.

Petrie, M. D., J. B. Bradford, R. M. Hubbard, W. K. Lauenroth, C. M. Andrews, and D. R. Schlaepfer. 2017. Climate change may restrict dryland forest regeneration in the 21st century. Ecology 98:1548–1559.

Petrie, M. D., A. M. Wildeman, J. B. Bradford, R. M. Hubbard, and W. K. Lauenroth. 2016. A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. Forest Ecology and Management 361:328–338.

Pierce, D. W., J. F. Kalansky, and D. R. Cayan. 2018. Climate, drought, and sea level rise scenarios for California's Fourth Climate Change Assessment. California's Fourth Climate Change Assessment, California Energy Comission. Publication Number: CNRA-CEC-2018-006.

Polade, S. D., A. Gershunov, D. R. Cayan, M. D. Dettinger, and D. W. Pierce. 2017. Precipitation in a warming world: Assessing projected hydro-climate changes in California and other Mediterranean climate regions. Scientific Reports 7:1–10.

Potter, D. A. 1998. Forested communities of the upper montane in the central and southern Sierra Nevada. PSW-GTR-169, USDA Forest Service, Pacific Southwest Research Station. Albany, California, USA.

Redmond, M. D., N. S. Cobb, M. J. Clifford, and N. N. Barger. 2015. Woodland recovery following drought-induced tree mortality across an environmental stress gradient. Global Change Biology 21:3685–3695.

Restaino, C., D. J. N. Young, B. Estes, S. Gross, A. Wuenschel, M. Meyer, and H. Safford. 2019. Forest structure and climate mediate drought-induced tree mortality in forests of the Sierra Nevada, USA. Ecological Applications 29:1–14.

Rodman, K. C., T. T. Veblen, T. B. Chapman, M. T. Rother, A. P. Wion, and M. D. Redmond. 2019. Limitations to recovery following wildfire in dry forests of southern Colorado and northern New Mexico, USA. Ecological Applications 30: e02001.

Romme, W. H., et al. 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon–juniper vegetation of the western United States. Rangeland Ecology & Management 62:203–222.

Rosenzweig, M. L. 1968. Net primary productivity of terrestrial communities : prediction from climatological data. The American Naturalist 102:67–74.

Rother, M. T., and T. T. Veblen. 2016. Limited conifer regeneration following wildfires in dry ponderosa pine forests of the Colorado Front Range. Ecosphere 7:e01594.

Russell, S. K., and E. W. Schupp. 1998. Effects of microhabitat patchiness on patterns of seed dispersal and seed predation of *Cercocarpus ledifolius* (Rosaceae). Oikos 81:434.

Safford, H. D., and J. T. Stevens. 2017. Natural Range of Variation (NRV) for yellow pine and mixed conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. PSW-GTR-256, USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Savage, M., P. M. Brown, and J. Feddema. 1996. The role of climate in a pine forest regeneration pulse in the southwestern United States. Ecoscience 3:310–318.

Savage, M., and J. N. Mast. 2005. How resilient are southwestern ponderosa pine forests after crown fires? Canadian Journal of Forest Research 35:967–977.

Savage, M., J. N. Mast, and J. J. Feddema. 2013. Double whammy: high-severity fire and drought in ponderosa pine forests of the Southwest. Canadian Journal of Forest Research 43:570–583.

Seaber, P. R., F. P. Kapinos, and G. L. Knapp. 1987. Hydrologic Unit Maps. Water-Supply Paper 2294, US Geological Survey, Denver, Colorado, USA.

Serra-Diaz, J. M., C. Maxwell, M. S. Lucash, R. M. Scheller, D. M. Laflower, A. D. Miller, A. J. Tepley, H. E. Epstein, K. J. Anderson-Teixeira, and J. R. Thompson. 2018. Disequilibrium of fire-prone forests sets the stage for a rapid decline in conifer dominance during the 21stcentury. Scientific Reports 8:1–12.

Shive, K. L., H. K. Preisler, K. R. Welch, H. D. Safford, R. J. Butz, K. L. O'Hara, and S. L. Stephens. 2018. From the stand scale to the landscape scale: predicting the spatial patterns of forest regeneration after disturbance. Ecological Applications 28:1626–1639.

Simeone, C., M. P. Maneta, Z. A. Holden, G. Sapes, A. Sala, and S. Z. Dobrowski. 2019. Coupled ecohydrology and plant hydraulics modeling predicts ponderosa pine seedling mortality and lower treeline in the US Northern Rocky Mountains. New Phytologist 221:1814–1830.

Stephens, S. L. 2001. Fire history differences in adjacent Jeffrey pine and upper montane forests in the eastern Sierra Nevada. International Journal of Wildland Fire 10:161–167.

Stephens, S. J., C. McGuire, and L. Sims. 2004. Conservation Assessment and Strategy for the California Golden Trout (Oncorhynchus mykiss aguabonita) Tulare County, California. California Department of Fish and Game, San Joaquin Valley and South Sierra Region, Sacramento, California, USA.

Stephenson, N. 1990. Climatic control of vegetation distribution: the role of the water balance. American Naturalist 135:649–670.

Stephenson, N. L. 1998. Actual evapotranspiration and deficit: Biologically meaningful correlates of vegetation distribution across spatial scales. Journal of Biogeography 25:855–870.

Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato, P. Morgan, and T. T. Veblen. 2018. Evidence for declining forest resilience to wildfires under climate change. Ecology Letters 21:243–252.

Stevens-Rumann, C. S., and P. Morgan. 2019. Tree regeneration following wildfires in the western US: a review. Fire Ecology 15:1–17.

Stoddard, M. T., D. W. Huffman, P. Z. Fulé, J. E. Crouse, and A. J. Sánchez Meador. 2018. Forest structure and regeneration responses 15 years after wildfire in a ponderosa pine and mixed-conifer ecotone, Arizona, USA. Fire Ecology 14:12.

Swain, D. L., D. E. Horton, D. Singh, and N. S. Diffenbaugh. 2016. Trends in atmospheric patterns conducive to seasonal precipitation and temperature extremes in California. Science Advances 2:1–14.

Swain, D., B. Langenbrunner, J. D. Neelin, and A. Hall. 2018. Increasing precipitation volatility in twenty-first-century California. Nature Climate Change 8:427–433.

Taylor, A. H. 2004. Identifying forest reference conditions on early cut-over lands, Lake Tahoe Basin, USA. Ecological Applications 14:1903–1920.

Taylor, K. E., R. J. Stouffer, and G. A. Meehl. 2012. An overview of CMIP5 and experimental design. Bulletin of the American Meteorological Society 93:485–498.

Tepley, A. J., J. R. Thompson, H. E. Epstein, and K. J. Anderson-Teixeira. 2017. Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. Global Change Biology 23:4117–4132.

Vaillant, N. M., and S. L. Stephens. 2009. Fire history of a lower elevation Jeffrey pine-mixed conifer forest in the eastern Sierra Nevada, California, USA. Fire Ecology 5:4–19.

van de Water, K. M., and H. D. Safford. 2011. A summary of fire frequency estimates for California vegetation before Euro-American settlement. Fire Ecology 7:26–58.

Vander Wall, S. B. 2008. On the relative contributions of wind vs. animals to seed dispersal of four sierra Nevada pines. Ecology 89:1837–1849.

Vander Wall, S. B., and R. P. Balda. 1981. Ecology and evolution of food-storage behavior in conifer-seed-caching corvids. Zeitschrift Für Tierpsychologie 56:217–242.

Wangler, M. J., and R. A. Minnich. 1996. Fire and succession of pinyon-juniper woodlands of the San Bernadino Mountains, California. Madrono 43:493–514.

Welch, K. R., H. D. Safford, and T. P. Young. 2016. Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone. Ecosphere 7:1–29.

Williams, A. P., et al. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change 3:292–297.

Witty, J. H., R. C. Graham, K. R. Hubbert, J. A. Doolittle, and J. A. Wald. 2003. Contributions of water supply from the weathered bedrock zone to forest soil quality. Geoderma 114:389–400.

Young, D. J. N., J. T. Stevens, J. M. Earles, J. Moore, A. Ellis, A. L. Jirka, and A. M. Latimer. 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. Ecology Letters 20:78–86.

Ziffer-Berger, J., P. J. Weisberg, M. E. Cablk, and Y. Osem. 2014. Spatial patterns provide support for the stress-gradient hypothesis over a range-wide aridity gradient. Journal of Arid Environments 102:27–33.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3258/full