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LETTER

Fire-catalyzed vegetation shifts in ponderosa pine and Douglas-fir forests of the western United States

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Abstract

Increased wildfire activity combined with warm and dry post-fire conditions may undermine the mechanisms maintaining forest resilience to wildfires, potentially causing ecosystem transitions, or fire-catalyzed vegetation shifts. Stand-replacing fire is especially likely to catalyze vegetation shifts expected from climate change, by killing mature trees that are less sensitive to climate than juveniles. To understand the vulnerability of forests to fire-catalyzed vegetation shifts it is critical to identify both where fires will burn with stand-replacing severity and where climate conditions limit seedling recruitment. We used an extensive dendrochronological dataset to model the influence of seasonal climate on post-fire recruitment probability for ponderosa pine and Douglas-fir. We applied this model to project annual recruitment probability in the US intermountain west under contemporary and future climate conditions, which we compared to modeled probability of stand-replacing fire. We categorized areas as ‘vulnerable to fire-catalyzed vegetation shifts,’ if they were likely to burn at stand-replacing severity, if a fire were to occur, and had post-fire climate conditions unsuitable for tree recruitment. Climate suitability for recruitment declined over time in all ecoregions: 21% and 15% of the range of ponderosa pine and Douglas-fir, respectively, had climate conditions unsuitable for recruitment in the 1980s, whereas these values increased to 61% (ponderosa pine) and 34% (Douglas-fir) for the future climate scenario. Less area was vulnerable to fire-catalyzed vegetation shifts, but these values also increased over time, from 6% and 4% of the range of ponderosa pine and Douglas-fir in the 1980s, to 16% (ponderosa pine) and 10% (Douglas-fir) under the future climate scenario. Southern ecoregions had considerably higher vulnerability to fire-catalyzed vegetation shifts than northern ecoregions. Overall, our results suggest that the combination of climate warming and an increase in wildfire activity may substantially impact species distributions through fire-catalyzed vegetation shifts.

1. Introduction

The combination of changing climate and altered disturbance regimes are leading to substantial impacts on forests globally (Johnstone *et al* 2016, Seidl *et al* 2017). In the western US, warming is affecting forest

ecosystems directly, through controls on tree recruitment, growth, and mortality (van Mantgem *et al* 2009, Restaino *et al* 2016, Davis *et al* 2019a), and indirectly, through an increased frequency and extent of tree-killing disturbances such as wildfires (Abatzoglou and Williams 2016, Littell *et al* 2018). Area

burned by wildfires, and in some regions the proportion of area burning at high severity, has increased substantially in recent decades (Miller *et al* 2009, Dennison *et al* 2014, Harvey *et al* 2016, Westerling 2016, Singleton *et al* 2019). These changes in wildfire activity, combined with warm, dry post-fire conditions, may undermine the longstanding resilience of forest ecosystems to wildfires, resulting in ecosystem transitions (Johnstone *et al* 2016, Davis *et al* 2018) or ‘fire-catalyzed vegetation shifts.’ We define fire-catalyzed vegetation shifts as a major change in dominant species or lifeforms (e.g. shifts from one forest type to another, or from forest to non-forest vegetation) that is expected due to climate change alone, but which is accelerated due to wildfire. Fire-catalyzed vegetation shifts will significantly impact the ecosystem services and economic values provided by forests in the western US (Coop *et al* 2020).

Stand-replacing fire can catalyze vegetation shifts during directional climate change that would otherwise take decades or centuries to unfold (Gavin *et al* 2013, Crausbay *et al* 2017) by killing mature trees that are less sensitive to warm, dry conditions than juveniles of the same species (Bell *et al* 2014, Dobrowski *et al* 2015). This discrepancy in climate tolerance between juveniles and adults, combined with the long lifespan of many tree species, can result in plant-climate disequilibrium (Svenning and Sandel 2013), where the dominant mature trees on a landscape do not reflect current climate conditions (e.g. Campbell and Shinneman 2017, Serra-Diaz *et al* 2018).

Assessing forest vulnerability to fire-catalyzed vegetation shifts requires quantifying both the likelihood of stand-replacing fire and the potential for climate to limit post-fire regeneration. Efforts to quantify the potential for fire-catalyzed vegetation shifts under current or future climate conditions are sparse (Coop *et al* 2020). However, results from the few studies conducted suggest that fire-catalyzed vegetation shifts could be an important contributor to the reorganization of species expected due to climate change (Liang *et al* 2017, Serra-Diaz *et al* 2018, Stralberg *et al* 2018, Parks *et al* 2019).

Failure of post-fire tree regeneration due to unsuitable climate conditions is a crucial component of fire-catalyzed vegetation shifts, yet empirical models of post-fire recruitment are rarely incorporated into estimates of fire-catalyzed vegetation shifts. Low post-fire recruitment across the western US in recent decades (e.g. Savage and Mast 2005, Stevens-Rumann *et al* 2018, Rodman *et al* 2020) reflects a variety of interacting biotic and abiotic factors, including climate change (Korb *et al* 2019, Stevens-Rumann and Morgan 2019). However, assessing the extent to which climate conditions limit post-fire tree regeneration requires quantifying the relationship between seasonal climate conditions during the year of germination and post-fire recruitment. We recently conducted such an assessment for two conifers that

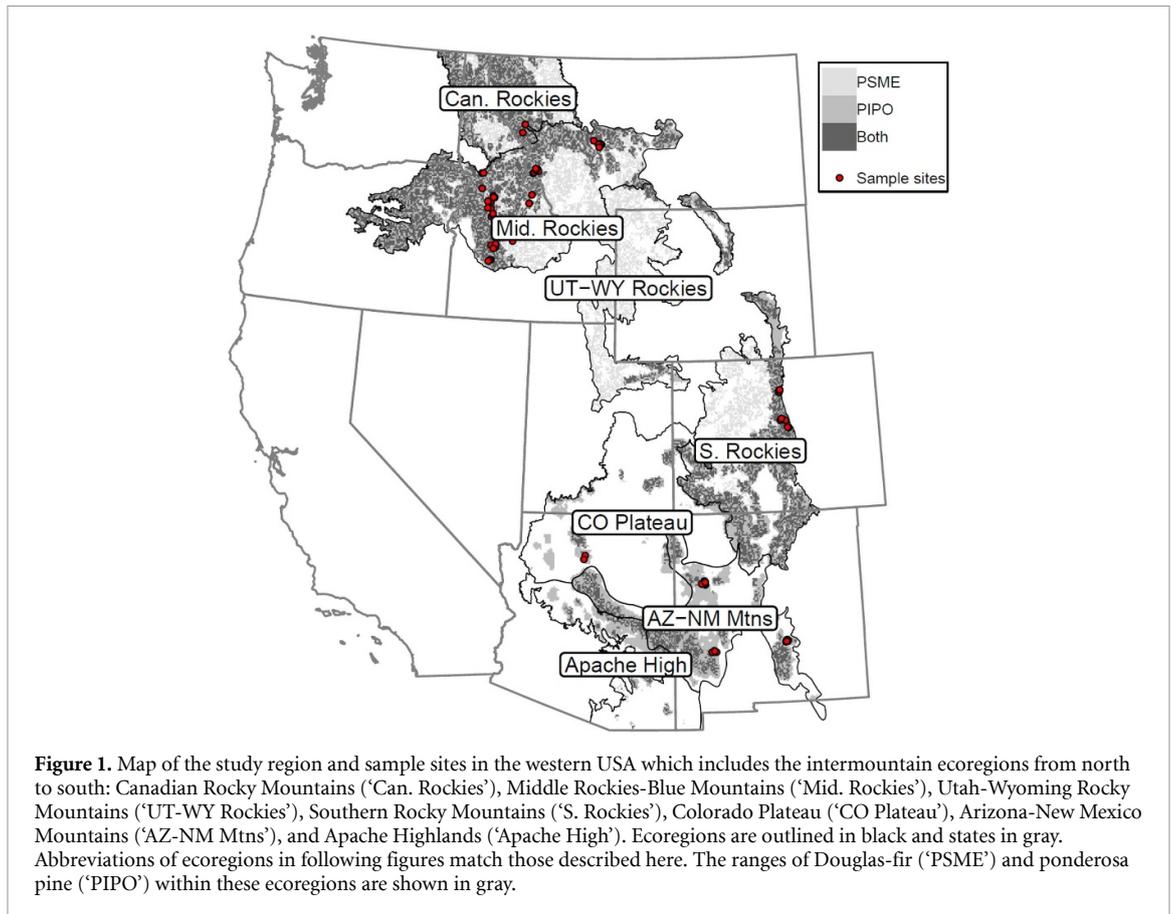
are dominant in low-elevation forests of western North America, ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*). Both species have traits that facilitate survival of low-intensity surface fires, including thick bark, but ponderosa pine is considered more fire resistant than Douglas-fir, due to self-pruning of lower branches and more flammable litter that promotes rapid fire spread and shorter residence times (Stevens *et al* 2020). Both species are vulnerable to mortality from crown fires. Ponderosa pine is shade intolerant, and in comparison, Douglas-fir is more shade-tolerant, with seedlings able to establish under and eventually overtop shrub cover, albeit with reduced growth rates (e.g. Shatford *et al* 2007, Tepley *et al* 2017). While the geographic range of the two species overlaps substantially, Douglas-fir occupies cooler and moister areas relative to ponderosa pine. In a warming field experiment, Douglas-fir seedling survival was lower in experimentally warmed plots compared to ponderosa pine (Rother *et al* 2015).

In our previous study, we found strong climatic thresholds to post-fire recruitment for both species. These climate thresholds have been crossed at sites near the warm, dry edge of the species’ distributions in recent years, suggesting that post-fire forest recovery will be unlikely in these areas (Davis *et al* 2019a). The extent of forests that are vulnerable to such post-fire regeneration failures, however, remains unclear. Such an assessment is critical for understanding the potential extent of fire-catalyzed ecosystem change and for developing and prioritizing possible management actions. Here we combine empirical relationships linking seasonal climate conditions to post-fire tree recruitment (*sensu* Davis *et al* 2019a) and projections of the likelihood of stand-replacing fire (Parks *et al* 2018) to quantify the vulnerability of ponderosa pine and Douglas-fir forests in the US intermountain west to fire-catalyzed vegetation shifts. We specifically ask: to what extent are ponderosa pine and Douglas-fir forests vulnerable to both stand-replacing fire and post-fire regeneration failure, and where is this vulnerability the highest under current and future climate?

2. Methods

2.1. Climate, fire, and tree-regeneration datasets

We used two existing datasets to quantify the components of fire-catalyzed vegetation shifts: a dataset quantifying where stand-replacing fires are likely to occur (Parks *et al* 2018), and a dataset of post-fire tree establishment dates (Rother and Veblen 2017, Davis *et al* 2019b) that allowed us to model the probability of post-fire tree regeneration. We focus on ponderosa pine and Douglas-fir because they are ecologically and economically important conifer species that are dominant in dry mixed-conifer forests across western North America.



To quantify where stand-replacing fires are likely to occur, we utilized a gridded dataset (Parks *et al* 2018) which predicts the probability of stand-replacing fire (for each 30 m cell), if a fire were to occur, under the average weather conditions during which areas burned in wildfires from 2002 to 2015. The predictions are derived from statistical models for each ecoregion that describe fire severity as a function of fuels (*i.e.* vegetation indices derived from Landsat imagery representing live fuel), topography, fire weather, and 30-yr climate normals. We first scaled these data up from 30 m to 4 km to match the resolution of the climate data, by taking the mean probability of high-severity fire across all 30-m cells. We then categorized cells as stand-replacing or non-stand-replacing following Parks *et al* (2019), who used unique probability thresholds for each ecoregion to create predictions that match the proportion of area burned with stand-replacing fire between 2002 and 2015.

To quantify the probability of post-fire tree establishment, we used a dendrochronological dataset of annually resolved establishment dates for 2180 ponderosa pine and Douglas-fir seedlings and saplings that regenerated following 26 fires that occurred between 1988 and 2007 (Rother and Veblen 2017, Davis *et al* 2019b). Trees that established in fires that burned prior to 1988 were too large to destructively sample, and we avoided fires after 2007 to allow at

least 9 years of post-fire regeneration. This dataset includes 39 sites in 17 fires in the northern Rockies, 10 sites in five fires in Colorado's Front Range, and 21 sites in four fires in the Southwest (figure 1). Sample sites were located at the warm, dry margin of the species' regional distributions, but still represented a large portion of the annual climate conditions experienced across the range of these species within the intermountain ecoregions (figures S1–4 (available online at stacks.iop.org/ERL/15/1040b8/mmedia)). Selected sites burned at moderate to high severity and had no post-fire planting. Seedlings and saplings were destructively sampled, cut into 2.5-cm segments above and below the root-shoot boundary, and processed and aged using standard dendroecological methods (see Davis *et al* 2019a, Rother and Veblen 2017 for further details).

Monthly, 4-km resolution climate data for each site from 1981–2015 were obtained from Terraclimate (Abatzoglou *et al* 2018). Future climate data were developed using a pattern-scaling approach that superposed the multi-model median change from an ensemble of 23 climate models (Qin *et al* 2020). Spatial scaling factors for each month and variable were calculated for each model as the differences in mean and standard deviation between late 21st century (2070–2099) and pre-industrial (1850–1879) per degree Celsius change in global mean temperature. We considered a climate scenario

Table 1. Seasonal climate variables evaluated in boosted regression tree (BRT) models of recruitment. “**” indicates the variable was retained in the final model for one of the species, and the relative influence of those variables in the final BRT models is shown.

Variable	Time window	Final model species	Relative influence
Precipitation (sum)	October–February	–	–
	March–May	–	–
	April–September	–	–
	June–August	–	–
	Annual	–	–
Maximum temperature (mean)	March–May	–	–
	April–September*	Douglas-fir	31%
	June–August	–	–
	Warmest month*	Ponderosa pine	17%
Vapor pressure deficit (mean)	April–September	–	–
	June–August*	Ponderosa pine	15%
	Warmest month	–	–
Climatic water deficit (sum)	April–September*	Douglas-fir	8%
	June–August	–	–
	Annual	–	–

where the global mean temperature reaches 2 °C above pre-industrial temperatures (1.3 °C warmer than the observational period), rather than using the traditional approach tied to specific emissions-policy trajectories. Future climate scenarios superposed projected changes in monthly scaling factors to observed data during 1985–2015 for individual climate variables. Further, we use a simple, non-species-specific approach to account for potential changes in plant water-use efficiency with rising CO₂ concentrations in reference evapotranspiration calculations (Kruijt *et al* 2008). Climate data is available here: www.climatologylab.org/terraclimate. Monthly maximum temperature, precipitation, vapor pressure deficit (VPD), and water-balance values were aggregated into seasonal and annual metrics (table 1).

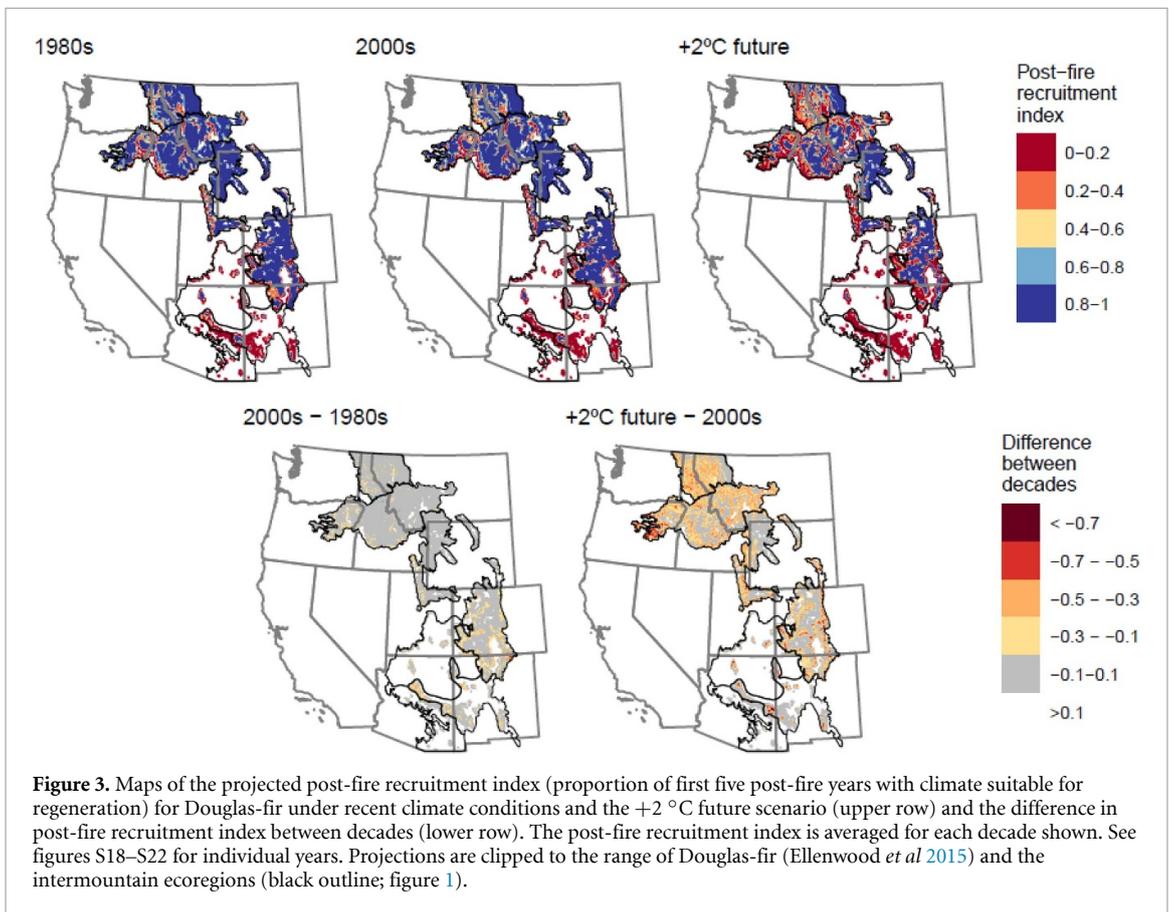
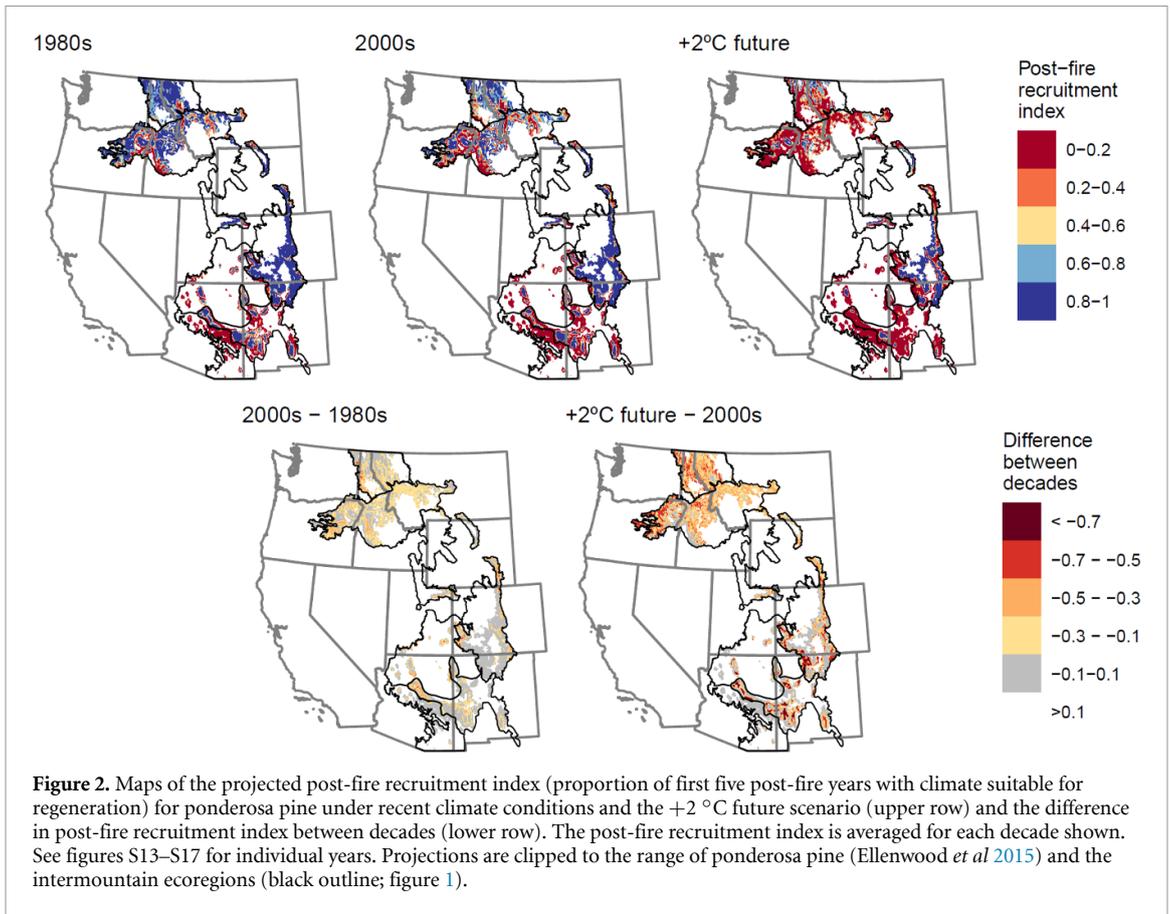
2.2. Statistical analysis

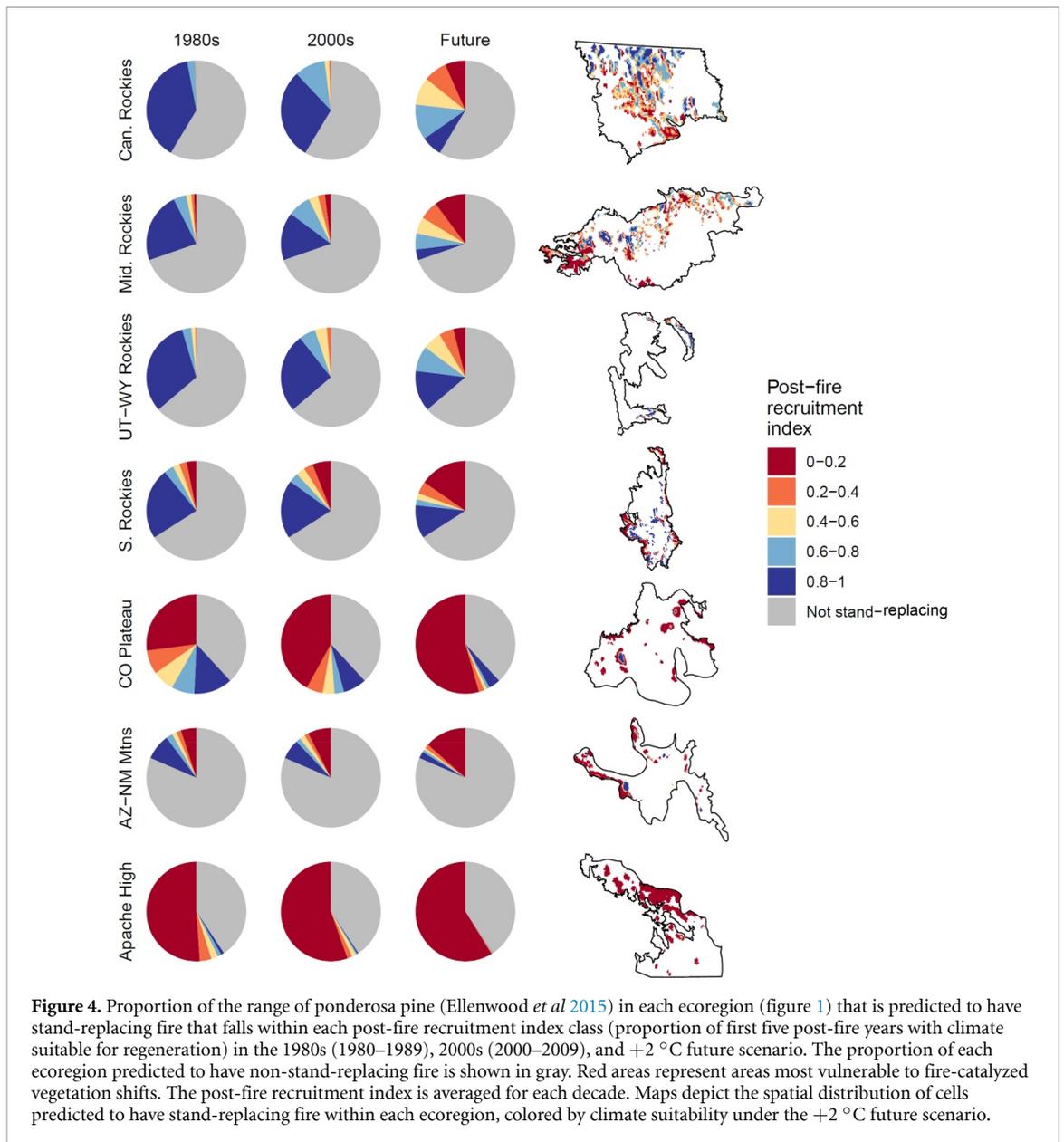
To model the relationship between annual recruitment and biophysical conditions at each site, we used boosted regression trees (BRT; Elith *et al* 2008) to model the probability of recruitment as a binomial response, with ‘success’ representing when annual recruitment (# juveniles ha⁻¹ yr⁻¹) exceeded a region- and species-specific density threshold (Davis *et al* 2019a). The region-specific threshold accounts for varying forest densities among regions and is defined as the 25th percentile of annual recruitment rates from among all years with recruitment for a given species in a given region (table S1). We also constructed BRT models with a 50th percentile threshold and with recruitment presence or absence alone and found similar results (figures S7–S10).

Each model contained static predictors, distance to seed source (measured in the field) and satellite-inferred fire severity for each plot (differenced normalized burn ratio (dNBR); Eidenshink *et al* 2007), and dynamic predictors that changed each year, time since fire and seasonal climate conditions. The initial models included the static variables, time since

fire, and a range of seasonal windows for each climate variable (maximum temperature, precipitation, VPD, and climatic water deficit) based on hypothesized importance to seedling recruitment (table 1). Based on relative influence in the initial BRT models, we selected the best seasonal window for each climate variable and constructed a new model with these seasonal climate predictors. We then selected which climate variables to include in the final model by using the function `gbm.simplify`, which performs backwards elimination of variables, dropping those with no evidence of improving predictive deviance (Elith *et al* 2008, Hijmans *et al* 2017).

We used our final models for each species to project post-fire recruitment probability (4 km resolution) across the range of ponderosa pine and Douglas-fir (Ellenwood *et al* 2015) within intermountain ecoregions of the western US (figure 1) from 1980–2014, and 10 years of a future scenario representing a +2 °C in global average temperatures relative to pre-industrial temperatures (scaled to years 2000–2009). For all projections, distance to seed source was held constant at 50 m, and dNBR (fire severity) was held constant at 400 (median across sites); a dNBR value of 400 loosely corresponds to the median tree mortality across sites, 92%. Seasonal climate conditions varied according to climate time series for each cell (4 km) and time since fire varied from 1 to 5 years, as described below. We chose a 5-year window because the majority (69%) of recruitment across all sites occurred within the first five post-fire years. For a hypothetical fire in each year, i , in each cell, we predicted the probability of post-fire recruitment in each of the first five post-fire years ($i + 1$ to $i + 5$). The probabilities were then classified as ‘recruitment’ or ‘lack of recruitment’ based on the threshold for each model that maximized specificity and sensitivity. Then, for each year i we calculated the proportion of the first five post-fire years that was climatically suitable for recruitment, yielding

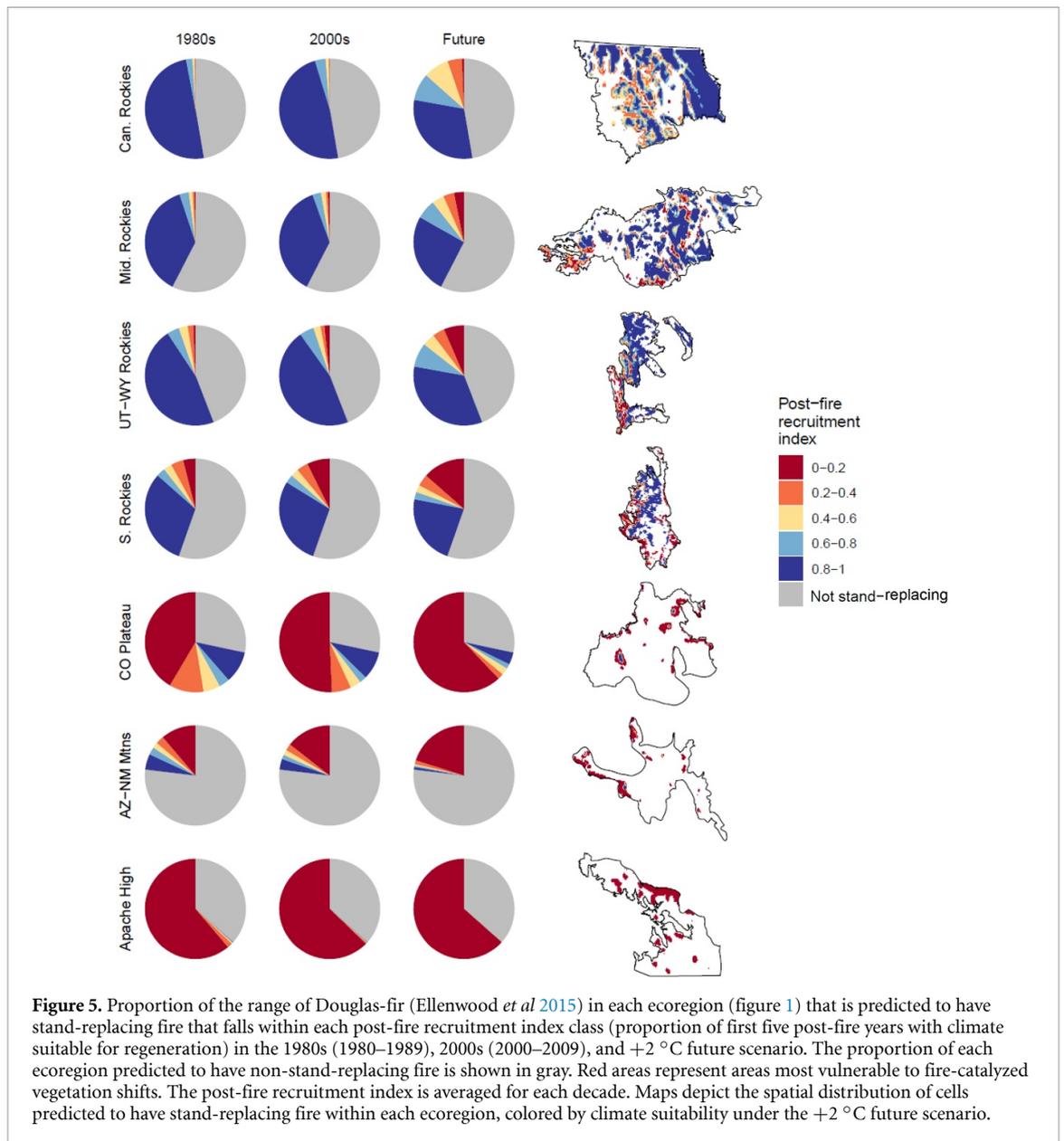




a value between 0 (no suitable years) and 1 (five suitable years); hereafter this is referred to as the post-fire recruitment index. Because we held distance to seed source and fire severity constant, the post-fire recruitment index is interpreted as the climate suitability for post-fire recruitment, under the given scenario. We recognize that post-fire recruitment is also influenced by other local factors that are unaccounted for in our models, including biotic interactions, such as herbivory and competition, and abiotic factors, such as substrate, topography and soil moisture (e.g. Korb *et al* 2019).

To calculate the proportion of each species' range within the intermountain west vulnerable to fire-catalyzed vegetation shifts under current and future climate conditions, we intersected the projections of stand-replacing fire from Parks *et al* (2018) with our

post-fire recruitment index, which we averaged by decade (1980–1989, 1990–1999, 2000–2009, 2010–2014, 10 years of the +2 °C future scenario). We considered cells to be vulnerable to fire-catalyzed vegetation shifts if the average post-fire recruitment index was less than 0.2 (*i.e.* on average fewer than one of the first five post-fire years were climatically suitable for regeneration) and they were predicted to burn at stand-replacing severity, if a fire were to occur. In our results, we highlight findings from three decades (1980–1989, 2000–2009, 10 years of the +2 °C future scenario) for the sake of space, see Supplemental Results for other years. Results with alternative cutoffs for the post-fire recruitment index (0 or <0.4) are also shown in tables S5 and S6. Our definition of fire-catalyzed vegetation shifts is broad, as 'shifts' could encompass changes from forest to non-forest in areas



where ponderosa pine and Douglas-fir make up the largest component of lower-treeline forests, or shifts to a different forest type or woodland, where other tree species currently exist at drier sites than ponderosa pine and Douglas-fir.

3. Results

Recruitment of both species had a nonlinear relationship with seasonal climate metrics (figures S5 and S6). The seasonal climate metrics included in the final model were mean summer (June–August) VPD and maximum temperature of the warmest month for ponderosa pine and growing season (April–September) water deficit and growing season mean maximum temperature for Douglas-fir. Recruitment was also negatively related to distance to seed source, time since fire, and, for ponderosa pine, fire severity.

The final models for both species had an AUC of 0.77 based on spatially stratified cross validation (by site).

Climate suitability for recruitment declined in the 2000s and the +2 °C scenario compared to the 1980s in all ecoregions (figures 2, 3 and S11–S24; tables S2–S3). Across all ecoregions, 21% and 15% of the range of ponderosa pine and Douglas-fir, respectively, had climate conditions unsuitable for recruitment in the 1980s. These values increased to 32% and 20% in the 2000s, and 61% and 34% under the +2 °C future climate scenario for ponderosa pine and Douglas-fir, respectively. Southern ecoregions had considerably lower climate suitability for post-fire recruitment than northern ecoregions. In contrast, northern ecoregions had a high proportion of area with climate conducive to post-fire regeneration in the 1980s and 2000s; however, there was a large decline in climate suitability under the +2 °C climate scenario.

Vulnerability to fire-catalyzed vegetation shifts increased across all ecoregions over time (tables S4 and S7–S8; figures 4–5). Across the study region, 6% and 4% of the area was vulnerable to fire-catalyzed shifts in the 1980s, for ponderosa pine and Douglas-fir, respectively. These numbers increased to 16% (ponderosa pine) and 10% (Douglas-fir) under future climate conditions. The Apache Highlands and Colorado Plateau ecoregions exhibited the highest vulnerability to fire-catalyzed vegetation shifts, while the three northernmost ecoregions exhibited the lowest vulnerability. While 14%–62% of the three northernmost ecoregions exhibited climate conditions unsuitable for post-fire recruitment under future climate conditions (tables S2–S3), these areas also tended to be more likely to burn at lower severity; thus, the overall vulnerability to fire-catalyzed shifts under future climate conditions in these ecoregions ranged from 1%–10%. Within each ecoregion, the lowest elevation areas within each species' distribution tended to have the lowest climate suitability for recruitment (figures S23–S24), but vulnerability to fire-catalyzed vegetation shifts tended to peak at intermediate elevations (figures S25–S26) due to an elevational trend in the probability of stand-replacing fire (figure S27).

4. Discussion

Our results highlight the potential for fire-catalyzed vegetation shifts to significantly alter forest ecosystems. Our findings suggest that more than 10% of the range of ponderosa pine and Douglas-fir within the US intermountain west may be vulnerable to such shifts in the coming years and decades, reflecting the climatic disequilibrium between where mature trees exist today and conditions required for tree recruitment. While we estimate that 34% (Douglas-fir) and 61% (ponderosa pine) of the current range of these species will become unsuitable for post-fire regeneration under a scenario of global mean temperatures +2 °C above pre-industrial levels, the proportion of the range vulnerable to fire-catalyzed vegetation shifts is lower, at 10% and 16%, respectively. This difference reflects the assumption that mature trees will persist across much of their range, given a lack of lethal fire. Nevertheless, a loss of ponderosa pine and Douglas-fir in even 10%–16% of their current range would likely have substantial impacts on the ecosystem services and economic activities provided by these widespread forest types (Coop *et al* 2020). Furthermore, in areas with less suitable climate for regeneration, but which are unlikely to experience stand-replacing fire, conversion to other species or vegetation types may occur due to other types of tree-killing disturbances such as insect outbreaks or drought-induced mortality (Seidl *et al* 2017, Lloret and Kitzberger 2018).

A key strength of our analysis is that it matches the relevant time scales of the biophysical processes

linking climate to post-fire tree recruitment. Specifically, we relate annual recruitment, rather than adult presence, to seasonal climate conditions, rather than 30-year average conditions. Following stand-replacing disturbance, recruitment is a critical demographic process that determines vegetation trajectories, and thus the regeneration niche is more relevant for predicting range shifts than the niche for adult survival (Jackson *et al* 2009). Due to the annual precision of our recruitment dataset, our projections incorporate the effects of interannual climate variability in the first five post-fire years. Interannual climate variability is particularly important when sites are close to climatic thresholds to recruitment, as such variability creates opportunities for episodic recruitment in particularly cool, wet years, even if conditions are, on average, too warm and dry for recruitment (Rother and Veblen 2017, Davis *et al* 2019a).

Our results indicate that the areas vulnerable to fire-catalyzed vegetation shifts are not homogeneously distributed across the range of ponderosa pine and Douglas-fir. Vulnerability is substantially higher in southern ecoregions, consistent with modeling results suggesting significant forest loss in the Southwest under future climate scenarios (Tarancon *et al* 2014, Yazzie *et al* 2019), and with patterns of tree regeneration. For example, low climate suitability for ponderosa pine projected in the southern ecoregions, even in the 1980s, is consistent with observations of episodic ponderosa pine recruitment coincident with cool, wet years (Savage *et al* 1996, Dugan and Baker 2015) and limited conifer recruitment following recent fires in this region (e.g. Savage and Mast 2005, Coop *et al* 2016, Rodman *et al* 2020). Populations such as these at the 'trailing edge' of species ranges are often disproportionately important for the survival and evolution of species, given their high genetic diversity (Hampe and Petit 2005). Thus gene conservation efforts for ponderosa pine are arguably most warranted in the Southwest (Potter *et al* 2015), where we show a substantial risk of fire-catalyzed loss of ponderosa pine under both current and future conditions. Although a lower proportion of the area in northern ecoregions was vulnerable to fire-catalyzed vegetation shifts, there was a larger projected increase in vulnerability in the future than in the southern ecoregions. These results agree with studies showing that many sites in the northern Rockies were still resilient to mixed severity fire in the 2000s (Kemp *et al* 2016), but are projected to see declines in recruitment under future climate conditions (Kemp *et al* 2019).

The implications of fire-catalyzed vegetation shifts for ecosystem processes and services depends on what vegetation communities transition to in the future (Coop *et al* 2020). In some areas, fire-catalyzed shifts in ponderosa pine and Douglas-fir forests may lead to non-forest vegetation, while in others it may lead to dominance of different forest types. For example, in northern ecoregions, where

ponderosa pine and Douglas-fir tend to comprise lower-treeline forests, loss of these two species may indeed represent forest loss; in this case, our projections of vulnerability to fire-catalyzed shifts are similar to previous projections of fire-catalyzed forest loss by Parks *et al* (2019). In contrast, in the three southernmost ecoregions, lower treeline is dominated by different forest or woodland types, including piñon pine (*Pinus* spp.) and juniper (*Juniperus* spp.), such that loss of ponderosa pine or Douglas-fir may not represent a loss of forest or woodland vegetation; consequently, our results suggest a higher proportion of area vulnerable to loss of ponderosa pine and Douglas-fir following fire than Parks *et al* (2019) predict as vulnerable to overall forest loss.

We found that vulnerability to fire-catalyzed species loss, locally, was greater for ponderosa pine compared to Douglas-fir overall (table S4), largely driven by differences in the northern ecoregions, and in agreement with niche models based on current adult distributions (Rehfeldt *et al* 2014a). The difference between species likely reflects the broad ecological amplitude of Douglas-fir, which can tolerate cooler and wetter conditions than ponderosa pine, but which is also fairly tolerant of moisture stress (Rehfeldt *et al* 2008). The current range of Douglas-fir extends into moister and cooler areas than that of ponderosa pine, which are more likely to maintain suitable climate for recruitment in the future. Consequently, ponderosa pine may need to disperse farther than Douglas-fir from its current range to encounter climate conditions suitable for regeneration in the future. Our results are indicative of the potential for fire-catalyzed range contraction at the warm dry margins of the current distribution of ponderosa pine and Douglas-fir; importantly, they do not capture the potential for fire to catalyze range expansion along the cooler and wetter range margins of these species (e.g. by reducing competition with existing vegetation). Some models predict fire will catalyze range expansion due to climate change (Stralberg *et al* 2018), while others suggest that dispersal may limit expansion into burned areas (Campbell and Shinneman 2017).

Our results should be interpreted in light of four main constraints. First, the climate data we used are at a relatively coarse resolution and therefore do not account for small-scale variability in climate due to topography (Dobrowski 2011) or canopy cover (Davis *et al* 2019c). Thus, even in an area that we model as having low recruitment probability, there may be microsites where recruitment probability is higher, and likewise, some areas projected to have high recruitment probability may have microsites with low recruitment probability (e.g. south-facing slopes). Second, sample sites represent warm, dry areas of the species' local distributions; thus, projections of recruitment in colder and wetter areas are not as reliable (figures S1–S4). There was also

some extrapolation to warmer conditions when making projections under the +2 °C climate scenario (figures S1–4); however, because the marginal relationships with climate flatten near climate extremes (figures S5 and S6), projections under warmer conditions than experienced in the past may overpredict recruitment probabilities. Third, we used fire severity projections under 'average weather conditions in which fires burn,' which likely underestimates the potential for fire-catalyzed vegetation shifts in the future, given that stand-replacing fires are more likely under the more extreme weather conditions expected in the future (Tang *et al* 2015, Parks *et al* 2018). Projections of fire severity assumed fuel loads from 2016, which may change over time, but given that our +2 °C climate scenario is expected to be realized mid-century, we do not expect large-scale shifts in forest structure and composition in the absence of stand-replacing disturbance. Finally, we held distance to seed source and fire severity constant across our projections of recruitment probabilities. The spatial patterns of our results are consistent across different levels of distance to seed source and fire severity, but the absolute values change. Our results highlight where climate limitation to recruitment may drive fire-catalyzed loss of ponderosa pine and Douglas-fir, but seed limitation and short-interval fires also have the potential to drive fire-catalyzed vegetation shifts, even where climate is suitable for recruitment (Davis *et al* 2018, Coop *et al* 2020).

4.1. Management implications and conclusions

Our results have direct implications for management aimed at maintaining ponderosa pine and Douglas-fir forests in the US intermountain west. For example, within most regions, particularly in the northern ecoregions, we expect that some areas will retain climate suitable for post-fire regeneration of these two species, even under the +2 °C climate scenario. In these areas, post-fire management can focus on reforestation where a seed source is lacking. Where climate is marginal for post-fire regeneration, managers conducting post-fire planting to maintain ponderosa pine and Douglas-fir on the landscape may consider implementing assisted gene flow (Aitken and Whitlock 2013) by planting seeds from warmer and drier sites (Rehfeldt *et al* 2014b), although uncertainties remain regarding the effectiveness of this strategy (Young *et al* 2020). In areas identified as climatically unsuitable for regeneration, it may be beneficial to emphasize pre-fire efforts to limit the occurrence of lethal fire or the size of stand-replacing patches (e.g. fuel reduction treatments), especially in areas where maintaining forest cover is particularly critical. However, stand-replacing fire is inevitable in at least some sites with climate unsuitable for regeneration, and in these areas, maintenance of ponderosa pine and Douglas-fir will be challenging, if not impossible. Managers will need to weigh

the acceptability of a vegetation transition versus the potentially high costs of mitigation (Higuera *et al* 2019). Where high mitigation costs are untenable, but forest is desired to achieve management goals, managers may need to consider planting species that are adapted to warmer and drier conditions than ponderosa pine and Douglas-fir, particularly in southern ecoregions and at low-elevation sites. In other situations, it may be desirable to accept or even facilitate fire-driven vegetation shifts (Mcwethy *et al* 2019), given that new vegetation types may actually be more resilient to future climate and fire conditions (Coop *et al* 2016).

Our results highlight the potential for the combined influences of climate warming and an increase in wildfire activity to substantially impact species distributions through fire-catalyzed vegetation shifts. Significant portions of ponderosa pine and Douglas-fir forests in the US intermountain west are vulnerable to fire-catalyzed vegetation shifts, and this vulnerability is projected to increase in upcoming decades as fires continue to burn more area under warmer, drier climate conditions (Abatzoglou and Williams 2016, Littell *et al* 2018). Given that regeneration of other tree species is also limited by warm, dry conditions (e.g. Conlisk *et al* 2017, Andrus *et al* 2018), fire-catalyzed vegetation shifts may also become more prevalent in other forest types (Coop *et al* 2020). Managers and society should expect changes, and prioritize responses accordingly, to best maintain and support services provided by forest ecosystems.

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Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: <https://doi.org/10.5061/dryad.pc3f9d8>.

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