ARTICLE

High-severity fire drives persistent floristic homogenization in human-altered forests

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Funding information
USDA Forest Service

Handling Editor: Franco Biondi

Abstract

Ecological disturbance regimes across the globe are being altered via direct and indirect human influences. Biodiversity loss at multiple scales can be a direct outcome of these shifts. Fire, especially in dry forests, is an ecological disturbance that is experiencing dramatic changes due to climate change, fire suppression, increased human population in fire-prone areas, and alterations to vegetation composition and structure. Dry western conifer forests that historically experienced frequent, low-severity fires are now increasingly burning at high severity. Relatively little work has been done looking at the effects of this novel disturbance type on affected plant communities, and little is known about how these impacts change over time. To fill in these knowledge gaps, we examined a fire that burned in a yellow pine and mixed conifer forest in the central Sierra Nevada in California, USA. We sampled at five time steps across the nine years following the fire (1, 3, 5, 8, and 9 years postfire). We found a generally unimodal relationship between fire severity and plant alpha and gamma diversity, but found that areas that burned at high severity supported progressively lower plant diversity as time since fire increased. Similarly, beta diversity decreased drastically through time for the high-severity areas, while remaining more static in the other severity classes. The combination of these findings indicates that significant floristic homogenization can result from high-severity fire in this ecosystem type. We also saw consistently lower diversity in unburned areas in comparison to area burned at low and moderate severity, underlining that both lack of fire and high-severity fire can have negative impacts on postfire plant diversity. Unburned areas that experienced forest thinning after the first sample year saw an increase in plant diversity over time, suggesting that some—but not all—of the effects of fire on plant diversity can be approximated through forest management.

KEYWORDS
biotic homogenization, disturbance ecology, forest biology, high-severity fire, plant diversity

INTRODUCTION

Ecological disturbances shape ecosystems and exert various influences on both the biotic and physical environments (Shinoda & Akasaka, 2020; Sousa, 1984; Whittaker & Levin, 1977). The roles that an ecological disturbance plays in an ecosystem depend to a great extent on the disturbance regime (the typical spatiotemporal characteristics of the disturbance and its impacts), or notable variations from that regime (White & Pickett, 1985). Changes in species abundances and species diversity are often the product of major alterations to long-reigning disturbance regimes (D'Antonio & Vitousek, 1992; Miller & Safford, 2020). For example, a typical result of increasing disturbance frequency or severity can be biotic homogenization, where landscape-scale biodiversity is reduced due to strong disturbance-driven filtering of the species pool (Olden & Rooney, 2006, Safford & Mallek, 2010). Biotic homogenization driven by changes to disturbance regimes is happening across the globe in many ecosystems, often caused by human-driven intensification of a given disturbance, invasion of exotic species and their effects on disturbance frequency or severity, or introduction of novel disturbances, including land use changes such as deforestation and fragmentation (D'Antonio & Vitousek, 1992; Olden & Rooney, 2006; Rogers et al., 2009; Vellend et al., 2007). Human-driven changes to natural fire regimes are among the most widespread and most concerning sources of biotic homogenization (Kelly et al., 2020). For example, changed fire regimes are driving decreases in herbaceous plant diversity in temperate prairies (Alstad et al., 2016), lichen diversity in mid-elevation conifer forest (Miller et al., 2018), woody species diversity in neotropical forests (Spínola et al., 2020), and plant and animal diversity in the North American steppe (Coates et al., 2016; Mahood & Balch, 2019). As the occurrence of novel/uncharacteristic wildfire increases around the globe (Kelly et al., 2020), it is crucial to understand the immediate and long-term effects of these disturbances on biotic communities.

Dry forests in temperate latitudes, especially those altered by humans via long-term fire suppression and global warming, are seeing some of the most notable changes in fire regimes (Abatzoglou & Williams, 2016; Mallek et al., 2013; Steel et al., 2015). Semiarid western US forests dominated by fire-resistant tree species such as ponderosa and Jeffrey pine (*Pinus ponderosa* and *Pinus jeffreyi*; collectively known as "yellow pine") supported fire regimes characterized by frequent, mostly low- and moderate-severity fires (fire severity is a measure of fire's effect on an ecosystem, often measured as biomass loss or plant mortality) before the arrival of Anglo-American settlers in the mid-19th century (Agee, 1993; Safford & Stevens, 2017; Van

Wagtendonk et al., 2018). However, after large-scale timber harvest, the devastation of native American populations (who used fire extensively as a management tool), and the imposition of fire exclusion policies in the early 20th century, fires in these forest types have become rare (Mallek et al., 2013; Safford & Van de Water, 2014; Steel et al., 2015). In combination with climatic trends, changes in forest density and composition, fuel loading and fuel continuity stemming from these actions make current and future fires progressively more likely to be large, high-severity events that result in ecosystem effects that are transformative rather than sustaining (Dove et al., 2020; Miller & Safford, 2012; Safford et al., 2022).

As high-severity fires become more common in dry forests (Miller et al., 2009; Singleton et al., 2019), it is critical to understand the long-term effects of these novel disturbance regimes. This is especially important in yellow pine and associated mixed conifer forests as (1) they are the forest types where the increase in fire severity is most pronounced (Mallek et al., 2013; Noss et al., 2006; Steel et al., 2015) and (2) such forests are widely distributed across the western United States (Barbour et al., 2000). Because large areas of high-severity fire were fairly novel in these ecosystems until recently, there is relatively little known about how they may affect plant community composition and species diversity (but see Miller & Safford, 2020; Richter et al., 2019). In yellow pine and mixed conifer forests (hereafter "YPMC" forests), plant communities that are adapted to a regime of high-frequency, low-severity fire are now experiencing fires that burn well outside of the historic range of variation (Bohlman et al., 2021; Safford & Stevens, 2017). Large, uncharacteristically severe disturbances can cause major shifts in ecosystem structure and in some cases may lead to long-term ecosystem conversion (Coppoletta et al., 2016; Tepley et al., 2017). A further issue is that relatively few plant species in YPMC forests possess adaptations to high-intensity burning, because such burning was historically rare (Keeley & Safford, 2016).

Given the lack of adaptations to high-intensity fire in most YPMC forests, the temporal shift toward less fire overall but higher severity burning when it occurs is likely to have a negative impact on plant diversity. Studies of the effects of fire intensity or severity on plant diversity in YPMC forest have historically focused primarily on controlled/prescribed fire conditions, and such studies typically find positive linear relationships between severity and plant diversity (Schoennagel et al., 2004; Wayman & North, 2007; Webster & Halpern, 2010). However, because prescribed fires are generally designed to avoid high-severity burning, these studies cannot evaluate the high end of the severity spectrum.

Recent studies in YPMC forests in the western United States burned by wildfires—which are more likely to include all levels of fire severity—have found that the disturbance × diversity relationship for plants is broadly negative beyond the moderate-severity peak (DeSiervo et al., 2015; Richter et al., 2019; Stevens et al., 2015), following general trends predicted by classical ecological disturbance theories like the intermediate disturbance hypothesis (Connell, 1978), Huston's dynamic equilibrium model (Huston, 1994), and patch-mosaic theory (Parr & Andersen, 2006). Miller and Safford (2020) reviewed these patterns for the western United States and suggested that they were related to the composition of the species pool and correlated with the extent to which the modern fire regime resembled the historical range of variation. However, Miller and Safford (2020) also noted that wildfire-based studies do not necessarily include all severity classes, often use space for time substitution, and usually only sample at one postfire time step, generally within a few years of the fire.

In this contribution, we take advantage of a high-density plot network and postfire sampling over a nine-year period to study how fire severity influences plant diversity after a wildfire in YPMC forest. In our study, we tested four main predictions. First, that alpha and gamma diversity would show a unimodal response to fire severity, with high-severity burn supporting reduced plant diversity in the years after fire (Miller & Safford, 2020; Richter et al., 2019). Second, we predicted that this general trend would hold through time, as the duration of our study was within the historical fire return interval, but that diversity in the high-severity areas would decrease through time as shrub cover increased and reduced species evenness (Bohlman et al., 2016; Welch et al., 2016). Third, because large areas of stand-replacing fire were historically rare in YPMC forests and severe disturbances tend to homogenize floras (Burkle et al., 2015), we predicted that areas burned in the large high-severity patches would have lower beta diversity. Finally, we predicted that these effects on beta diversity would also persist through the nine years of our study, because the effects of high-severity fire on forest structure persist for several decades (Nagel & Taylor, 2005).

METHODS

Study site

Our study site is located in El Dorado County, California, in the Lake Tahoe Basin (LTB). The climate is Mediterranean type with cool, wet winters and warm, dry summers. Mean annual precipitation at the nearby South Lake Tahoe Airport is about 500 mm, with approximately 80%, falling between October and March, primarily as snow. The January mean minimum temperature is −8.8°C and the July mean maximum is 27.1°C (WRCC, 2020). Elevations within the study site range from 1950 to 2200 m. The soils are mostly gravelly, originating from glacial till and outwash, with slopes ranging from 0% to 70% (SoilWeb, 2020). Geologic source rock for the glacial deposits is mostly Mesozoic granitoid rocks, with a minor component of Mesozoic metamorphic rocks (Saucedo, 2005).

Vegetation at the site is dominated by YPMC forest. The overstory is comprised mainly of Jeffrey pine (*P. jeffreyi*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), red fir (*Abies magnifica*), and lodgepole pine (*Pinus contorta*). Several shrub species from the genera *Arctostaphylos* and *Ceanothus* are present in gaps in the forest, along with other shrubs and many herbaceous species; large expanses of shrubs currently occupy previous areas of forest that were severely burned. Besides isolated areas of cheatgrass (*Bromus tectorum*), invasive plants are relatively rare within the site.

The Angora Fire

The Angora Fire burned 1300 ha (13 km^2) just south of South Lake Tahoe from June 24 to July 2, 2007. Early summer conditions in the Sierra Nevada were unusually dry with spring snowpack at approximately 30% of the long-term average. Burning in the Angora Fire was very severe, with about 53% of the area burning at high severity (>75% canopy tree mortality; Safford et al., 2009). Steep slopes, high winds, dense forest stands, and high fuel loads interacted with the very dry conditions to contribute to the high severity and resistance to control (Safford et al., 2009). Due largely to its easy accessibility and moderate size, the Angora Fire is one of the most studied wildfires in the United States, with the permanent plot network within it being used for a variety of ecological and management-based research (e.g., Carlson et al., 2012; Dalrymple & Safford, 2013; Safford et al., 2009, 2012; Stevens et al., 2014, 2015; Tarbill et al., 2018; White et al., 2016).

Management history

Between 1996 and 2006, the US Forest Service carried out approximately 194 ha of vegetation treatment within the Angora Fire footprint (Safford et al., 2009). Management was focused on reducing fire spread rate and flame length

and lowering fire risk to neighborhoods adjacent to Forest Service lands, principally by surface and ladder fuel reduction and some canopy thinning. Most treatments were followed by activity fuel piling and subsequent burning. The percentage of our study plots that were thinned prior to the Angora Fire are as follows: 48% of low-moderate-severity plots, 53% of moderate-severity plots, 13% of high-severity plots, and 19% of very-high-severity plots.

In the years following the fire, a variety of management actions continued to be implemented in and around the fire area. For this project, we were most concerned with postfire management that may have marked effects on postfire plant community diversity. We binned management activities in three categories: "Unmanaged" included minor removals of trees such as incidental cuts and firewood or local use cuts that would have little to no impact on plant diversity; "Lightly Thinned" referred to forest thinning activities in the plot that did not exceed 20% of trees; and "Heavily Thinned" plots were those that had experienced thinning that removed over 20% of trees. The total number of our study plots increased between the initial and third time steps (one and five years postfire) due to new plots being established. Decreases in the following years were due to several plots being so heavily managed that they were no longer recognizable in the field (Table 1).

Study plot establishment

Plots were sited on the vertices of a 400-m grid overlaid on the fire area in GIS using Landsat RdNBR (relativized delta normalized burn ratio) data (Miller & Thode, 2007) to estimate fire severity at each plot. Approximately equal numbers of plots were established in areas experiencing 0%–50%, 50%–75%, 75%–90%, and >90% postfire overstory mortality. Control (unburned) plots were randomly sited in vegetation analogous to the prefire plant community around the outside of the fire perimeter. Plots were circular with a radius of 16 m (804 m^2 [0.2 acre] in area). Plots were initially established one-year postfire (2008). Revisits were carried out at three-, five-, eight-, and nine-year postfire (2010, 2012, 2015, and 2016).

Plot protocol

On the initial plot visits in 2008, fire severities estimated using the RdNBR satellite data were validated and translated to the inverse of the National Park Service fire effects monitoring scale, as in Welch et al. (2016; see Table 2). Rebar stakes with labeled plastic caps were installed at plot centers to facilitate relocation in following years. Plot sampling followed a modified Common Stand Exam (CSE) protocol (USDA Forest Service, 2012),

TABLE 1 Management classification and plot distributions within category.

Years after fire	Unmanaged	Lightly thinned	Heavily thinned	Total no. managed	Total no. plots
One	40	16	15	31	71
Three	45	17	16	33	78
Five	32	22	32	54	86
Eight	31	16	37	53	84
Nine	26	14	40	54	80

Note: Numerical values indicate the number of plots in each unique combination of time-since-fire and management category. Additional control plots were added at three and five years postfire, which account for the increased number of overall plots. At eight and nine years postfire, plots were eliminated from sampling if they were managed so heavily as to be unrecognizable (e.g., heavy mastication and vehicle use that eliminated nearly all understory vegetation).

TABLE 2 Fire severity classification used for ground-truthing remotely sensed severity estimates (adapted from Welch et al., 2016).

Fire severity class (designation)	Description	Percentage basal area mortality
0: Unburned	Unburned	0
1: Low-moderate	Lightly burned, no significant overstory mortality, patchy spatial burn pattern, groups of surviving shrubs/saplings, or isolated overstory mortality, most saplings/shrubs dead	0–50
2: Moderate	Moderately burned, mixed overstory mortality, understory mortality burned to the ground	50–75
3: High	High intensity, significant proportions (75%–100%) of overstory killed, dead needles remaining on trees one year later	75–90
4: Very high	High-intensity burn, total/near-total mortality of overstory, most needles consumed in fire	>90

with detailed measurements of trees, fuels, coarse woody debris, ground cover, understory, and species richness and cover; see Safford et al. (2009) and Carlson et al. (2012) for details. For this study, we focus on data collected on species composition and cover. Every sampling year, ocular estimates for percent cover of all present plant species were made at each plot.

Data analysis: Alpha and gamma diversity

We tested the effects of burn severity, time since fire, topographic position index (TPI; a proxy for plot-level water availability), and precipitation on species richness and Shannon diversity using generalized linear models fit with the BRMS package. Management (as a binary variable) was included in early analyses but failed to increase model certainty. Burn severity was modeled as a five-level categorical variable (from unburned to high severity). Time since fire and precipitation were modeled as interacting with burn severity to reflect the hypotheses that their effects are dependent on fire effects. Precipitation in a given water year was included as a percentage of the 30-year average, and June–August precipitation as a percentage of the 30-year average for that time period. Plot ID was included as a random intercept to account for repeated measures across years. All continuous predictors were scaled with a mean of 0 and a SD of 1. We used a Poisson error structure in the species richness model and a Gaussian error structure in the Shannon diversity model. All analyses were completed in the R statistical language (R Code Team, 2021).

Gamma richness was calculated using averaged rarefied richness from the vegan package in R statistical software (R Code Team, 2021). To calculate the exponentiated Shannon's index, we summed the cover (proportionally) for each class (Jost, 2006).

Data analysis: Beta diversity

To explore possible postfire floristic homogenization patterns, we performed pairwise comparisons between each possible combination of plots for every unique combination of year and fire severity class using Bray–Curtis dissimilarity. We then plotted the mean dissimilarity for each unique fire severity and year combination.

To assess compositional beta diversity, we used the vegan package in R (R Code Team, 2021), to run a nonmetric multidimensional scaling (NMDS) ordination to determine the relationship (relative overlap of species) between fire severity classes through time. Using Bray–Curtis dissimilarity, we calculated pairwise

differences between all observations across all fire severity classes and years, in order to maintain visual comparability across years. To create the data visualization, we subset by year. We generated the NMDS using 999 iterations or until convergence was achieved.

RESULTS

Alpha diversity

Model results show highest richness and Shannon diversity among the plots of the low-moderate and moderate fire severity classes (<50 and 50%–75% canopy cover loss). For species richness, there was no clear effect of time since fire, with only the unburned class showing a significant increase over time (Figure 1). Shannon diversity showed potential but nonsignificant increases with time for the unburned and low-moderate classes. More obvious were significant declines in Shannon diversity with increasing time since fire for moderate- to very-high-severity classes. Furthermore, the effect size increased at higher levels of burn severity, indicating a greater rate of diversity loss in the highest severity classes (Figure 1). Both species richness and Shannon diversity showed slightly negative but nonsignificant responses to increasing TPI (less water availability; Appendix S1: Figure S4).

In our model, the percent of 30-year average annual precipitation had no discernible effects on richness or diversity with one notable exception. Shannon diversity was higher in relatively wet years among low-moderate-severity plots (Appendix S1: Figure S1).

Gamma diversity

When assessing species richness within severity classes, a generally unimodal relationship between fire severity and diversity was present across all years (Figure 2). The highest overall species richness was consistently observed within the low-moderate- and moderate-severity classes, except for the first year after fire, when richness was predictably highest in the unburned plots. For all years, the lowest gamma richness was found in the very-high-severity class with the exception of three years postfire when it was slightly more diverse than the high-severity and unburned groups. Overall, we observed the highest number of plant species at eight years postfire. When weighting richness and evenness equally to calculate the exponential Shannon diversity index, the highest diversity was found in the low-moderate and moderate fire severity classes in most years (Figure 2). From 2012
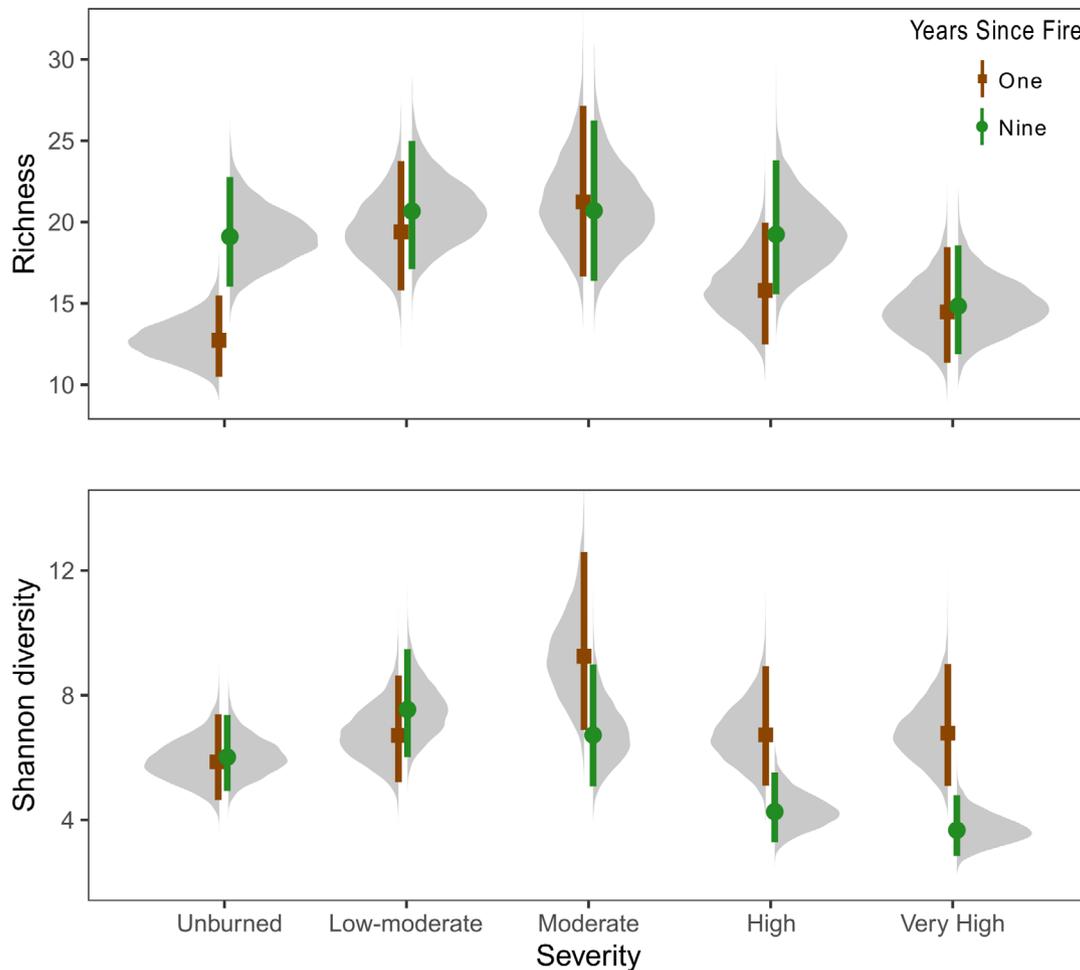
FIGURE 1   Marginal effects plot of burn severity and time since fire for species richness and Shannon diversity. To illustrate the interaction of severity and time since fire, model predictions are shown for 1 year since fire (brown square and lines; left-hand distributions), and 9 years since fire (green circles and lines; right-hand distributions). Gray areas represent the full distribution of model predictions. The points are the mean estimate, and the bars are the 95% confidence intervals. Topographic position index and precipitation are held at their mean values to display marginal effects.

onward, much lower Shannon diversity was observed in the high- and very-high-severity classes than in the other classes.

Beta diversity

In the first year postfire, there was no discernable relationship between beta diversity (species turnover among plots within a severity class) and fire severity (Figure 3). The pattern transitioned to a unimodal relationship by five years postfire. Over the course of the study period, beta diversity generally increased in the unburned and low-moderate-severity plots, rose and then fell in the moderate-severity plots, and decreased in the high and very-high-severity plots. By eight and nine years postfire, beta diversity in the unburned to moderate-severity classes was much higher than in the high and very high classes.

Using Bray–Curtis dissimilarity, which takes species abundance into account, a temporal pattern of plant community divergence between fire severity classes developed between the initial and final sampling years (one and nine years postfire, respectively; Figure 4). Fire severity accounts for 5% of the community variation at one-year postfire ($p = 0.002$) and between 13% and 18% for the following years (p values ≤ 0.001). With a k value of 2 and a stress of 0.25, this analysis can be used as a visualization tool, rather than deriving purely statistical inferences. Postfire communities were relatively similar at the initial sampling time step, then diverged (Figure 4). By nine years postfire, there was major differentiation between the unburned, low-moderate-, and moderate-severity classes on the one hand, and the high- and very-high-severity classes on the other. Community divergence is also noticeable within the unburned, low-moderate-, and moderate-severity classes, but the
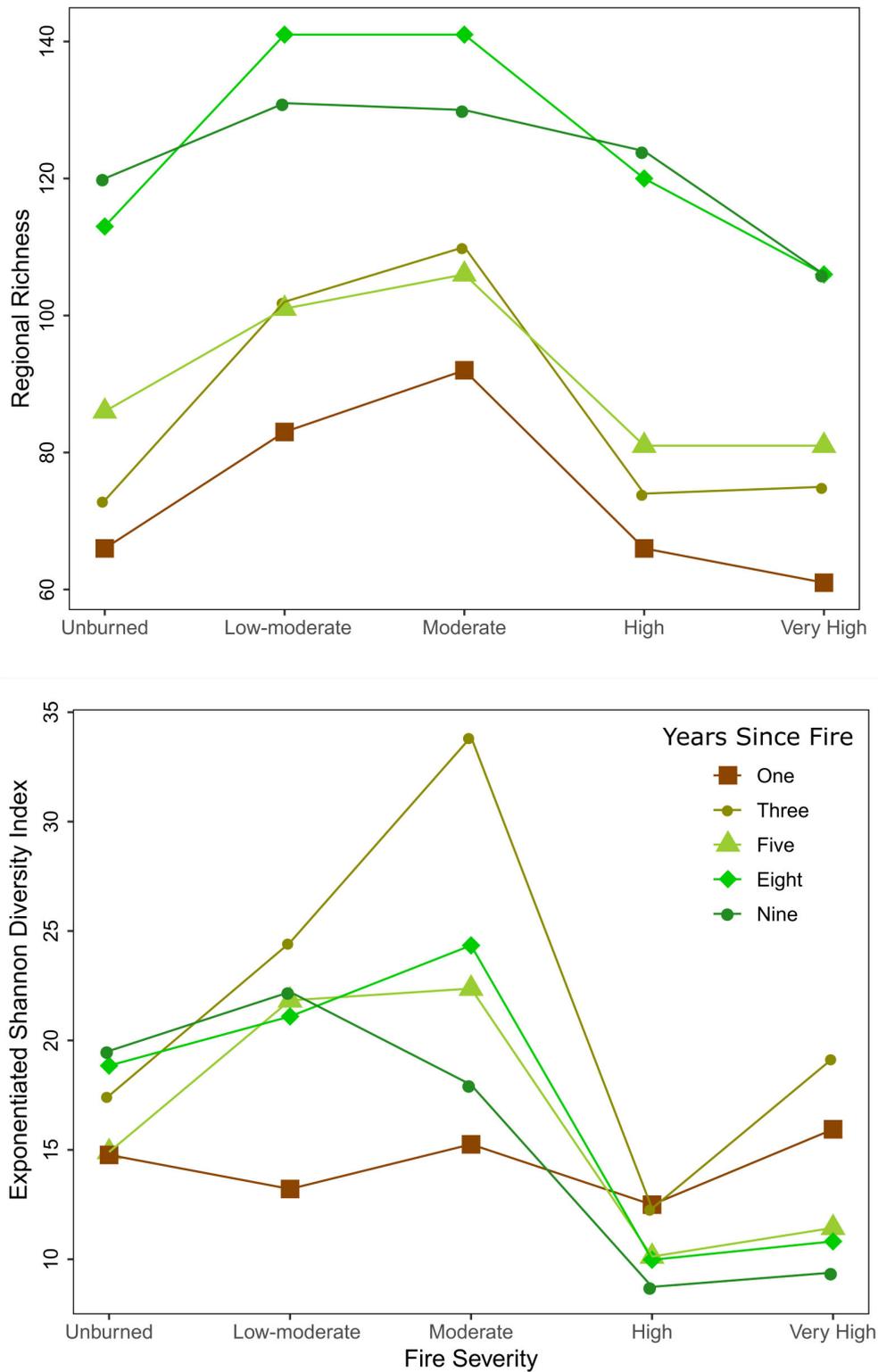
FIGURE 2 Gamma diversity across sampling years and severity of the Angora Fire as measured by rarefied species richness and Shannon diversity.

ellipses representing their 95% confidence intervals continue to overlap. Plots within each fire severity class were clustered together and remained clustered over time, but the amount of overlap between classes changed as time

progressed. All classes had significant overlap in the first year after fire, but over the following years, two distinct clusters formed: an unburned, low-moderate, and moderate classes cluster, and a high- and very-high-severity
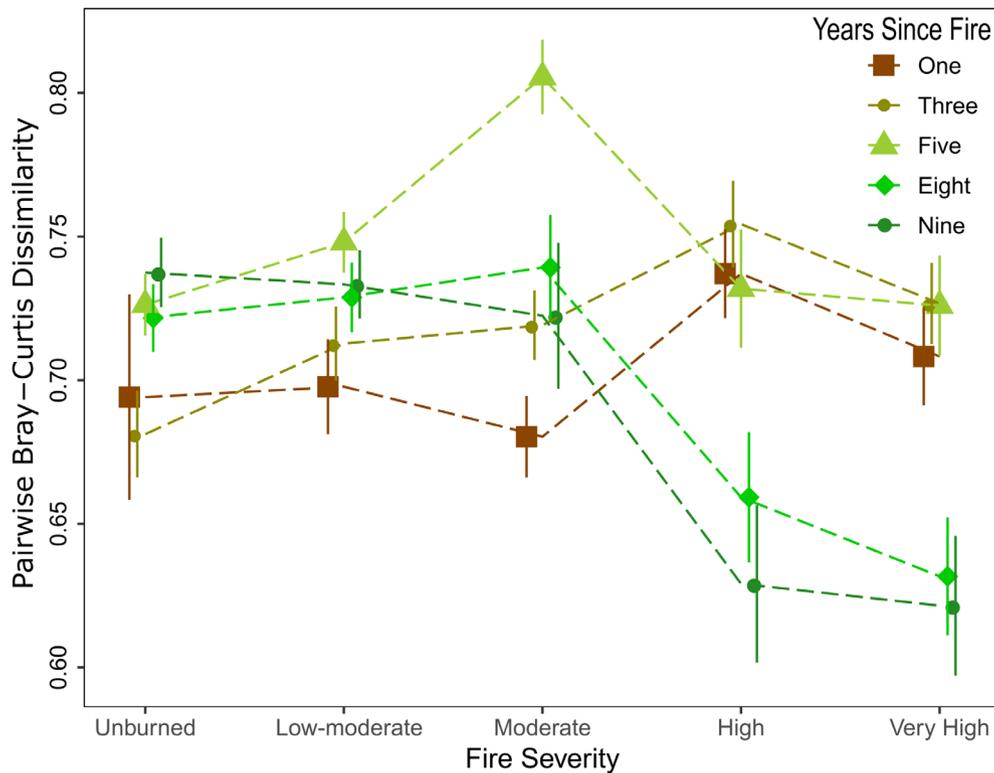
FIGURE 3 Beta diversity using pairwise Bray–Curtis dissimilarity (mean ± SE).

class cluster. Areas burned at high and very high severity were dominated by a few shrub species from the genera *Ceanothus* and *Arctostaphylos*, with the most prevalent species of each genus (*C. cordulata* and *A. patula*) having combined covers of between 80% and 90% in many plots (Appendix S1: Figure S6). Shrub dominance in these areas is increasing through time.

DISCUSSION

Our study provides some of the strongest evidence that shifts toward higher fire severity can cause long-persisting floristic homogenization in forest ecosystems that are adapted to low- to moderate-severity fire. We found that the negative effects on plant richness and diversity caused by high-severity fire in YPMC forests not only continued but intensified up to nine years after fire. Initial strong unimodal relationships between diversity (both alpha and gamma) and fire severity persisted throughout the study period. In addition, our beta diversity measure (and the Shannon index diversity results) showed much higher variation in composition in the unburned, low-moderate, and moderate-severity plots than in the high- and very-high-severity plots. At nine years postfire, the high- and very-high-severity plots continue to be dominated by a few species of shrubs whose regeneration is stimulated

by high-intensity fire, either through germination of an existing seed bank or by resprouting from persistent lignotubers after the aboveground plant material is damaged (James, 1984; Kauffman, 1986; Kauffman & Martin, 1990; Keeley, 1991; Appendix S1: Figures S3 and S6, Table S1).

We found that the unimodal response of richness to fire severity was conserved through time, which substantiates previous work from this system (DeSiervo et al., 2015; Miller & Safford, 2020; Richter et al., 2019; Stevens et al., 2015). However, in our study, increasing time since fire intensified the negative effects of high-severity fire on diversity. This suggests that in systems that experienced low- and moderate-severity fire historically and were subsequently fire suppressed, there is a severity threshold above which fire's effect on a community will have marked long-term effects. Our beta diversity and NMDS analyses also indicate that the effects of high-severity fire on plant communities in yellow pine–mixed conifer forests are fundamentally different than those of low-moderate- and moderate-severity fire. Although there is little empirical evidence of ecological tipping points being caused by a single driver (Dudney & Suding, 2020), multiple compounding factors—such as shifts in forest structure and composition followed by uncharacteristically severe fire—can lead to significant and lasting landscape changes (Benedetti-Cecchi et al., 2015; Millar & Stephenson, 2015).
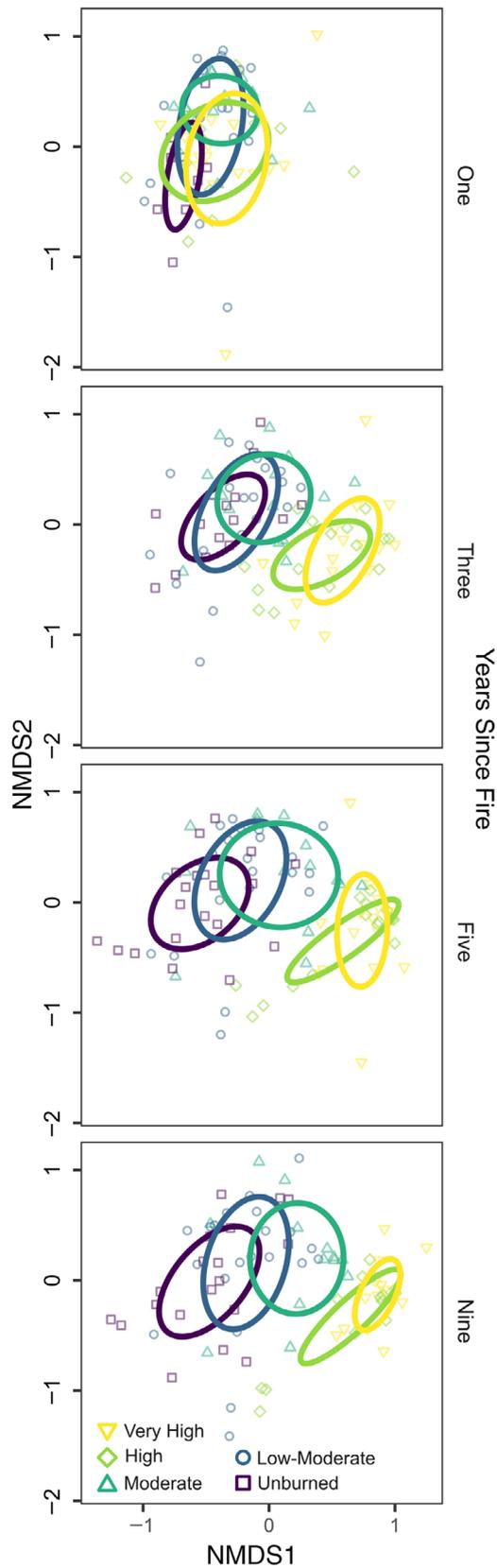
FIGURE 4 Nonmetric multidimensional scaling using Bray–Curtis dissimilarity. Symbols represent plots, and the ellipses represent the 95% confidence interval around the centroid for each severity class. Eight years postfire not depicted due to similarity with the previous and following sample years.

Our results show strong evidence of biotic homogenization over time in the high- and very-high-severity classes. In comparison to alpha and gamma diversity, in which unimodal responses of diversity to severity were found, beta diversity showed a distinctly different pattern, with drastically lower turnover among plots occurring in the high- and very-high-severity classes eight and nine years postfire when compared with earlier years. Reduced alpha and beta diversity when overstory mortality was >75% suggests that significant losses in plant diversity may occur across a landscape with large patches of high severity. The prediction that unburned plots would also have lower beta diversity was not supported by our analysis. This may be attributed in part to the dispersal of the unburned plots around the perimeter of the fire, which resulted in a larger range of elevation among plots and inter-plot distances that were much higher than in any of the other severity classes (i.e., the unburned plots sampled a larger landscape; see Richter et al., 2019). Additionally, the thinning treatments that took place in some of the unburned plots through the duration of our study (Table 1) added structural heterogeneity and increased light incidence at the soil surface, which contributed notably to the elevated alpha, beta, and gamma diversities in this class over time (Figures 1–3).

Our ordination analysis showed that plant communities in different fire severity classes diverged in the years after fire. The lack of community reconvergence by decade postfire coupled with the continued lack of conifer seedlings in many of the high- and very-high-severity plots (see Welch et al., 2016) points to the potential for long-term vegetation-type conversion to shrublands in these areas (McDonald & Fiddler, 2010). This will become even more likely if the site burns again in the near future (Coppoletta et al., 2016; Tepley et al., 2018), which is progressively more probable under current and projected fire and climate trends (Restaino & Safford, 2018).

The observed loss of diversity at the landscape scale (gamma diversity) under high- and very-high-severity burning can be attributed to reduction of both local diversity and species turnover. Both of these mechanisms were highly influenced by the extreme dominance of a handful of shrub species in the severely burned areas (Appendix S1: Figure S6). As shown by Stevens et al. (2015), more drought-tolerant plant species tend to be found in areas that experienced higher severity fire, while drought-intolerant plant species are more prevalent in unburned areas. Areas that experience moderate fire severity can sustain both of these groups and therefore have a larger species pool to draw from (Stevens et al., 2015). High- and very-high-severity areas are

contributing unique species to the overall species pool of the entire burned area, but relatively few compared with the number found in the other areas combined (Appendix S1: Figure S8). Gamma level richness was highest across all severities at eight and nine years postfire, but when evenness is accounted for, we see a peak at three years postfire and then a leveling off in the following years. As time progresses, more plants have the opportunity to establish (potentially causing richness to increase), but simultaneously evenness is progressively reduced by the increasing dominance of fire-stimulated shrubs (Bohlman et al., 2016; McDonald & Fiddler, 2010; Richter et al., 2019).

Results from our nine-year dataset demonstrate that management of forest fuels can positively impact plant diversity. All of the plots we sampled that burned at low-moderate severity and most that burned at moderate severity—those groups where we found the highest plant diversity—did so because of prefire fuel reduction by the Forest Service (Safford et al., 2009; Stevens et al., 2014). In contrast, essentially all high- and very-high-severity plots were found in areas where no prefire management had occurred and forest conditions before fire were characterized by high stem densities (especially of fire-intolerant species like *A. concolor*), high canopy cover, and heavy fuel loading. The marked gradient in postfire vegetation succession and structural and compositional heterogeneity is obvious in the photo set (Appendix S1: Figure S3a,b) and correlates with patterns of alpha, beta, and gamma diversity (Figures 1–3). Although these results may seem logical and predictable, there are few concrete demonstrations of this effect in the literature (but see Stevens et al., 2015), largely because most consideration of interactive effects of forest management and fire on plant diversity has occurred in prescribed fire scenarios. In addition, when we took fire severity, TPI, and precipitation into account, the only plot group that saw a lasting increase in local species richness after one-year postfire was the unburned control group. Almost all of our control plots were unmanaged when we first sampled them at one-year postfire, but many of them saw some level of surface and ladder fuel reduction and moderate canopy thinning in subsequent years. By reducing surface litter and overstory shading and by moderately disturbing the soil, these treatments played a similar role as low- to moderate-severity fire by increasing habitat for understory species. Previous work has suggested that fuel reduction treatments in YPMC forests rarely have negative impacts on plant diversity, and that positive impacts are more likely where fire is included in the treatment (Barefoot et al., 2019; Collins et al., 2007; Matzka & Kellogg, 1999;

McIver et al., 2012; Winford et al., 2015). Our results support this generalization, as in our study plant diversity was higher in areas burned at low-moderate severity (i.e., locations that were both thinned and burned) than in areas thinned but not burned (managed portion of the unburned class).

CONFLICT OF INTEREST STATEMENT
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data (Weeks, 2022) are available from Dryad: https://doi.org/10.25338/B8ND1W.

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SUPPORTING INFORMATION

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

How to cite this article: Weeks, JonahMaria, Jesse E. D. Miller, Zachary L. Steel, Evan E. Batzer, and Hugh D. Safford. 2023. "High-Severity Fire Drives Persistent Floristic Homogenization in Human-Altered Forests." *Ecosphere* 14(2): e4409. https://doi.org/10.1002/ecs2.4409