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Altered fire regimes cause long-term lichen diversity losses

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Abstract

Many global ecosystems have undergone shifts in fire regimes in recent decades, such as changes in fire size, frequency, and/or severity. Recent research shows that increases in fire size, frequency, and severity can lead to long-persisting deforestation, but the consequences of shifting fire regimes for biodiversity of other vegetative organisms (such as understory plants, fungi, and lichens) remain poorly understood. Understanding lichen responses to wildfire is particularly important because lichens play crucial roles in nutrient cycling and supporting wildlife in many ecosystems. Lichen responses to fire have been little studied, and most previous research has been limited to small geographic areas (e.g. studies of a single fire), making it difficult to establish generalizable patterns. To investigate long-term effects of fire severity on lichen communities, we sampled epiphytic lichen communities in 104 study plots across California's greater Sierra Nevada region in areas that burned in five wildfires, ranging from 4 to 16 years prior to sampling. The conifer forest ecosystems we studied have undergone a notable increase in fire severity in recent decades, and we sample across the full gradient of fire severity to infer how shifting fire regimes may influence landscape-level biodiversity. We find that low-severity fire has little to no effect on lichen communities. Areas that burned at moderate and high severities, however, have significantly and progressively lower lichen richness and abundance. Importantly, we observe very little postfire lichen recolonization on burned substrates even more than 15 years after fire. Our multivariate model suggests that the hotter, drier microclimates that occur after fire removes forest canopies may prevent lichen reestablishment, meaning that lichens are not likely to recolonize until mature trees regenerate. These findings suggest that altered fire regimes may cause broad and long-persisting landscape-scale biodiversity losses that could ultimately impact multiple trophic levels.

KEYWORDS
climate change, cryptic degradation, deforestation, disturbance, dry forests, epiphytes, interval squeeze, regime shifts

1 | INTRODUCTION

Wildfire plays a crucial role in regulating biodiversity and vegetation structure in many global ecosystems, but anthropogenic influences have changed fire regimes (e.g. fire frequency, severity, and size) in many parts of the world (Cochrane et al., 1999; Harvey, Donato, & Turner, 2016; Miller, Safford, Crimmins, & Thode, 2009; Prichard, Stevens-Rumann, & Hessburg, 2017). Departures from historical disturbance regimes are an important component of global change and can potentially cause widespread ecosystem changes and biodiversity losses (Dale et al., 2001; Enright, Fontaine, Bowman, Bradstock,

& Williams, 2015). In western North America, increases in fire size and severity in recent decades are linked to a warming climate, which can cause drier fuels and longer fire seasons and, in some ecosystems, a legacy of fire suppression that has increased fuel loads (flammable material in forests such as woody debris; Westerling, Hidalgo, Cayan, & Swetnam, 2006; Miller et al., 2009; Steel, Safford, & Viers, 2015). In some areas, these larger, hotter fires have led to vegetation shifts such as the conversion of formerly forested areas to shrublands or grasslands (Billings, 1994; Welch, Safford, & Young, 2016). However, relatively little is known about how altered fire regimes affect vegetative biodiversity in forest ecosystems, including understory plants, fungi, and lichens. These effects could include both direct effects of fire and indirect effects, such as community changes mediated by altered environmental conditions that result from postfire vegetation structure (Mistry, 1998); however, the relative contribution of direct and indirect effects of wildfire on lichen communities has not been previously tested.

Understanding lichen responses to fire is especially important because lichens are a crucial component of many global ecosystems. Lichens can play essential roles in forest nutrient cycling and in some cases provide up to 50% of plant-available nitrogen (Denison, 1973). Lichens are key components of forest food webs, providing an important food source and nesting material for mammals, birds, and innumerable invertebrates (Gerson & Seaward, 1977; Maser, Maser, & Trappe, 1985; Pettersson, Ball, Renhorn, Esseen, & Sjöberg, 1995). Lichens moderate forest hydrologic dynamics, gradually soaking up and then releasing water passively as ambient humidity changes (Gauslaa, 2014). Despite the presence of diverse lichen communities in nearly every terrestrial ecosystem, studies of lichen responses to fire have been few and have mostly occurred in boreal or tundra ecosystems (e.g. Johnson, 1981; Klein, 1982; Coxson & Marsh, 2001; Boudreault, Bergeron, & Coxson, 2009). Most previous studies of fire effects on lichens have also been restricted to small geographic areas (e.g. a single fire), making it difficult to establish generalizable patterns.

Lichens are known to be generally sensitive to fire, and epiphytic (bark-dwelling) lichens are likely to be entirely consumed in high-severity (i.e. stand-replacing) fires (Romagni & Gries, 2000). Although early-successional lichens may establish rapidly after fire on charred wood (Mistry, 1998; Park, Lichens, & Eversman, 2001; Romagni & Gries, 2000), lichen communities may take as long as 100 years or more to return to prefire community composition and abundance after high-severity fire (Boudreault et al., 2009). Indeed, lichen communities often reach greatest abundance and diversity in old growth forests where long-undisturbed wood substrates are available (e.g. tree boles and decorticated wood; Petersen et al., 2017). Although there is some evidence that even low-severity fire can decrease epiphytic lichen diversity (Ray, Barton, & Lendemer, 2015), low-severity fires can reduce stand density, which may be beneficial to lichen diversity in some cases (Root, McCune, & Neitlich, 2010). Many forests that have historically experienced frequent, primarily low-severity fire contain substantial epiphytic lichen communities, suggesting that such historical fire regimes have been generally compatible with

the long-term persistence of lichens at least at landscape scales, if not at finer scales. Shifts in fire regimes, however, raise questions about the future of these lichen communities.

The consequences of altered fire regimes for lichens may be particularly significant in light of expected effects of climate change on lichen communities. Climate envelopes for lichens are rapidly shifting, suggesting that large areas of contemporary lichen ranges may become inhospitable, potentially leading to range shifts or contractions (Allen & Lendemer, 2016; Nascimbene et al., 2016; Rubio-Salcedo, Psomas, Prieto, Zimmermann, & Martínez, 2016). Organisms often experience the strongest and most limiting environmental filters in the establishment life phase, and establishment has been shown to limit lichen distributions (Werth et al., 2006). This raises the question of whether wildfires that eliminate established epiphytic lichens across broad landscapes could catalyze range contractions if lichens are unable to reestablish after fire. As postfire landscapes generally contain warmer, drier microclimates due to reductions in canopy cover (Ma, Concilio, Oakley, North, & Chen, 2010), postfire lichen establishment could be particularly inhibited by a warming climate. Lichens may be especially sensitive to such environmental changes because of their small stature and dependence on ambient resources.

In this study, we examine lichen diversity patterns after wildland fires in mid-elevation conifer forests in the Sierra Nevada and Warner Mountains of California, USA. We hypothesized that fire would cause greater decreases in lichen diversity with increasing fire severity, as the ecosystem is historically adapted to fire characterized by a preponderance of low-severity effects (Safford & Stevens, 2017; a more detailed discussion of fire regimes follows). We also hypothesized that lichen diversity would be positively correlated with overstory tree canopy cover and tree height, as the lower abundance of trees produces a warmer, drier microclimate in the postfire landscape that may be less suitable for lichens than shady forest habitats. To test these hypotheses, we sampled lichen communities across the full gradient of fire severity (including unburned control plots) in areas that burned in five different fires across a broad area of Northern California, with sampling occurring at 4–16 years after fire.

2 | MATERIALS AND METHODS

2.1 | Lichen biology and dispersal

In this study, we focus on epiphytic (bark- and wood-dwelling) lichen communities. Lichens are symbiotic organisms that contain at least one fungal partner (the "mycobiont") and at least one photosynthesizing partner (the "photobiont," a green alga or cyanobacteria). "Macrolichens" are lichens with three-dimensional growth forms that are not completely appressed to a substrate, such as foliose (leaf-like) and fruticose (hair-like) lichens. Lichen growth rates are variable among species and depend on variables such as light and water availability. Measured as linear lobe expansion, macrolichens have been shown to grow roughly 0.5–5 mm/year, although there have been numerous observations outside of this range (Nash, 2008).

Lichen species reproduce either sexually or asexually; some species use both reproductive modes. Sexual reproduction involves the production of fungal spores, which must encounter a compatible species of free-living photobiont in the environment to form a new lichen thallus. Asexual reproduction occurs via propagules that contain both the mycobiont and photobiont, meaning that new lichens may be able to grow from asexual propagules without having to encounter an appropriate partner in the environment. Asexual propagules are generally larger than fungal spores and disperse shorter distances (Goward, 2011). Lichens may increase forest fire risk in part by acting as ladder fuels (Menning & Stephens, 2007). For more details on lichen biology, please see Nash (2008).

2.2 | Study system

To characterize lichen responses to altered fire regimes, we sampled postfire lichen communities in semiarid, mid-elevation (~1,800–2,500 m) conifer forests in the Sierra Nevada and Warner Mountains of California (Figures 1 and 2a,b). The mixed conifer forests we sampled included yellow pine (*Pinus jeffreyi* and *Pinus ponderosa*) at lower elevations, and a greater component of red fir (*Abies magnifica*) at higher elevations, with some plots in pure or nearly pure red fir

stands. Other common trees in our study areas included incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), and western white pine (*Pinus monticola*). Epiphytic lichen communities in these forests (Figure 2c) have low diversity compared to wetter forest systems (Jovan, 2008), but can reach substantial biomass (Rambo, 2010).

2.3 | Historical fire regimes

Yellow pine and mixed conifer forests historically burned relatively frequently, primarily at low-to-moderate severity (e.g. ground fires with infrequent and patchy tree crown burning; Agee, 1993; Sugihara, Wagtendonk, Shaffer, Fites-Kaufman, & Thode, 2006; Safford & Stevens, 2017). In part because of decades of fire suppression that have increased fuel loads (flammable vegetative biomass), these forests now experience much more stand-replacing (high-severity) fire than they did historically (Mallek, Safford, Viers, & Miller, 2013; Steel et al., 2015). Red fir forests historically burned at intermediate frequencies and moderate severities and have experienced modest shifts toward less frequent, more severe fires in recent decades as well, although they represent less of a departure from historical conditions than yellow pine forests (Mallek et al., 2013; Steel et al.,
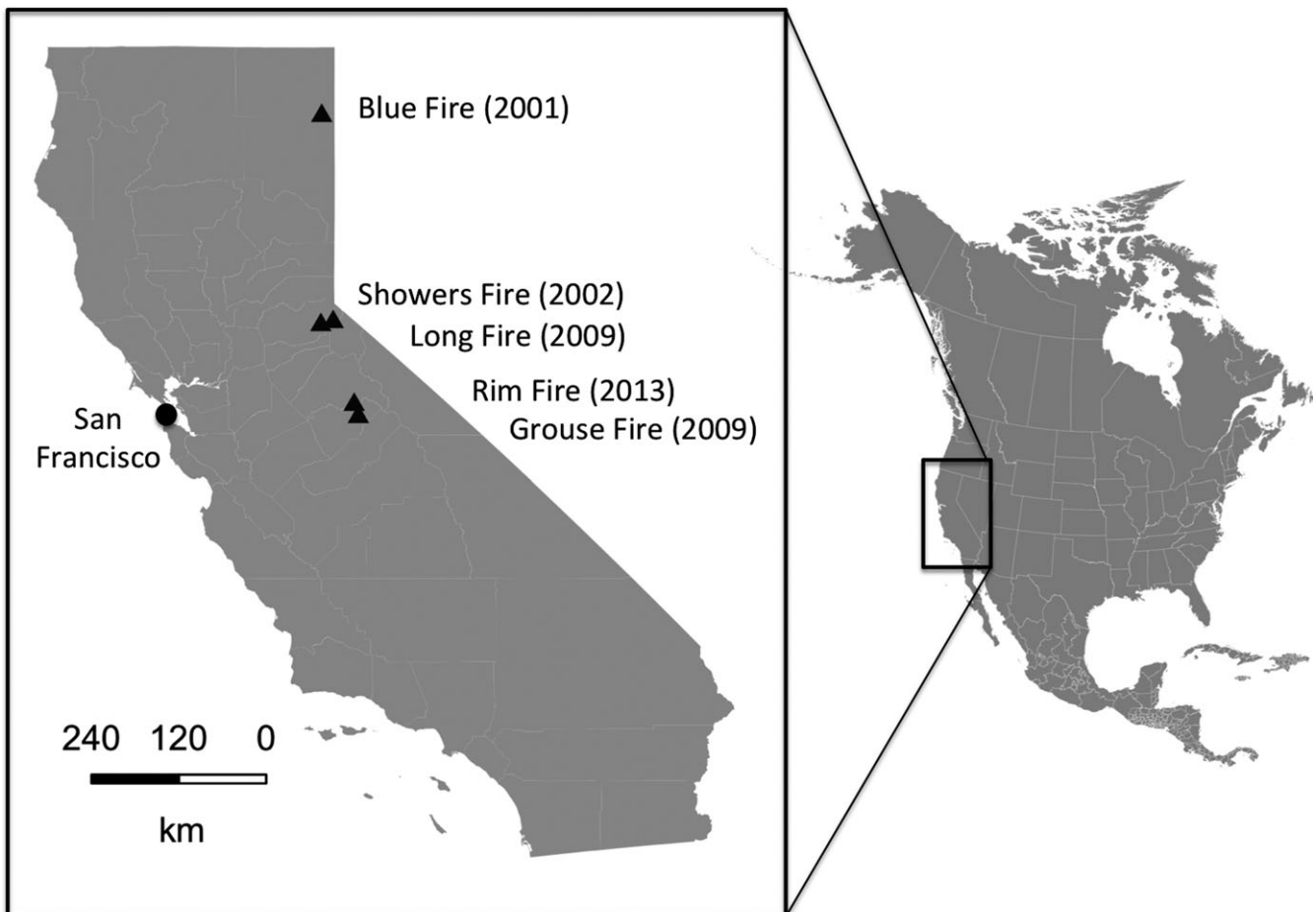
FIGURE 1 Map of the five fires we studied in the Sierra Nevada and Warner Mountains of California, USA

FIGURE 2 Photographs of study areas and organisms: (a) Relatively dense unburned stand of red fir and white fir near the area that burned in the Grouse Fire, (b) a large, high-severity burn patch that remains deforested 16 years after the Blue Fire, and (c) typical epiphytic macrolichen community from an unburned site adjacent to the Blue Fire

2015; Safford & van de Water, 2014). The size of high-severity burn patches has also increased in yellow pine and mixed conifer forests, today commonly creating large deforested areas (>100 ha) in post-fire landscapes (Safford & Stevens, 2017). Deforested areas, especially at lower elevations within our study area, are typically dominated by dense shrubs within five years after fire and in some cases persist as shrublands for decades (Welch et al., 2016).

2.4 | Site selection

Within each fire, we established 18–27 study plots across the full spectrum of fire severity (Supporting Information Figure S1). In each fire, we attempted to sample at least three plots in each of the four fire severity levels: unburned, low (classes 1–2), moderate (class 3), and high (classes 4–5). We used vegetation maps from Forest Service existing vegetation mapping (EVEG; https://www.fs.usda.gov/main/r5/landmanagement/gis, accessed 2016–2017) to identify areas with yellow pine, mixed conifer, and red fir forest vegetation for sampling. To identify study locations across the full spectrum of fire severity, we used maps of the relativized differenced normalized burn ratio (RdNBR), which is based on LANDSAT imagery and represents change in vegetation cover after fire. We obtained these spatial fire severity data from the USDA Forest Service (available online at https://www.fs.usda.gov/main/r5/landmanagement/gis, accessed 2016–2017). Because remotely sensed fire severity data are prone to some misclassification error (Miller & Thode, 2007), these data were used for site selection only, and all fire severity assessments used in subsequent analysis were based on field measurements, as in Welch et al. (2016). We attempted to sample plots with similar ranges of slope and aspect across the fire severity gradient to minimize confounding environmental factors. Plot locations were randomly or arbitrarily selected by placing points on a map prior to field

surveys. Plots were located >200 m apart. Unburned reference plots were located adjacent to burn areas in areas of forest that were similar to estimated forest conditions in burned areas prior to fire (i.e. generally midseral stands). Because almost all productive montane forests in the Sierra Nevada have a history of logging, our study sites may not represent the maximum potential lichen diversity for the region, which would probably occur only in old growth forests (Petersen et al., 2017). We believe, however, that they are generally representative of contemporary forest conditions in the Sierra Nevada.

2.5 | Sampling protocol

We sampled lichen communities using circular, 406 m^2 study plots following a modified version of the Forest Service common stand examination protocol (USDA, 2015). In each plot, we recorded all epiphytic macrolichen species that occurred. In addition to searching for lichens growing on tree boles and low branches, we included lichens found in litterfall if they appeared to have originated in the plot. Lichen diversity in litterfall has been shown to be coarsely representative of forest canopy lichen diversity, although lichens that are present at very low abundance in the canopy may not be detected in litterfall (Miller, Villella, Carey, Carlberg, & Root, 2017). Specimens that could not be identified to species in the field were collected for laboratory identification. Lichen abundance was characterized using the forest inventory and analysis lichen plot abundance scoring method where each species is given a ranking between one and four, representing increasing abundance (Britton, Mitchell, Potts, & Genney, 2014). We also noted whether lichens had colonized burned substrates in the period after fire in each plot.

Fire severity was characterized in the field using an inverse version of the US National Park Service's fire severity scale (slightly

modified from Welch et al., 2016; Supporting information Table S1). We visually estimated canopy cover of living trees and measured the average overstory tree height in the plot using a laser rangefinder. To characterize site environmental variation, we recorded slope and aspect, which we used to calculate heat load for analysis. Heat load is a single variable representing topographic effects on site microclimate; it is based on solar radiation, with an adjustment to account for afternoons being hotter than mornings (McCune & Keon, 2002).

2.6 | Statistical analysis

We began analysis by exploring relationships among variables of interest using scatterplots and boxplots (Figure 3). We used ANOVA to test for a bivariate relationship between fire severity and lichen richness; in this analysis, fire severity classes 1 and 2 were combined as "low severity" and classes 4 and 5 were combined as "high severity" to simplify interpretation. We used regression to test for bivariate relationships between lichen richness and tree canopy cover, tree height, and heat load. All data exploration and analysis was conducted in R (R Core Team, 2016).

We used structural equation modeling to test hypothesized relationships about drivers of lichen richness in postfire landscapes. Structural equation modeling is an analytic approach that can evaluate hypotheses about complex networks of cause–effect relationships in natural systems. One advantage of structural equation modeling is that it allows both direct and indirect relationships (i.e. relationships that are modulated by a third variable) to be evaluated. We evaluated structural equation models using the piecewiseSEM package (Lefcheck, 2016), which allows multiple linear mixed models to be combined into structural equation models. This approach allowed us to account for among-fire variation in lichen richness using random effects.

We followed Grace's (2006) recommended approach for developing structural equation models. We began by creating a "meta-model" that included hypothesized relationships among variables. Our structural equation meta-model contained three endogenous variables—lichen richness, tree canopy cover, and average tree height—and two exogenous variables, heat load and fire severity. We then evaluated the model using data and refined it by removing one path. We also explored model configurations that included quadratic terms for tree canopy cover and average tree height, but because including these variables produced models that were not consistent with the data (model p-value <0.05), we did not ultimately include them. To improve variable normality and better meet model assumptions, we square-root-transformed tree overstory cover, transformed average tree height by raising it to the 0.75 power, and transformed heat load by raising it to the sixth power. We modeled the ordinal fire severity variable as a continuous variable as recommended by Grace (2006).

3 | RESULTS

We sampled 104 study plots across the five fires. Across all plots, lichen richness ranged from zero to eight species (Figures 3 and 4; a full species list is given in Supporting Information Table S2). Overall, there was no significant difference in lichen richness between
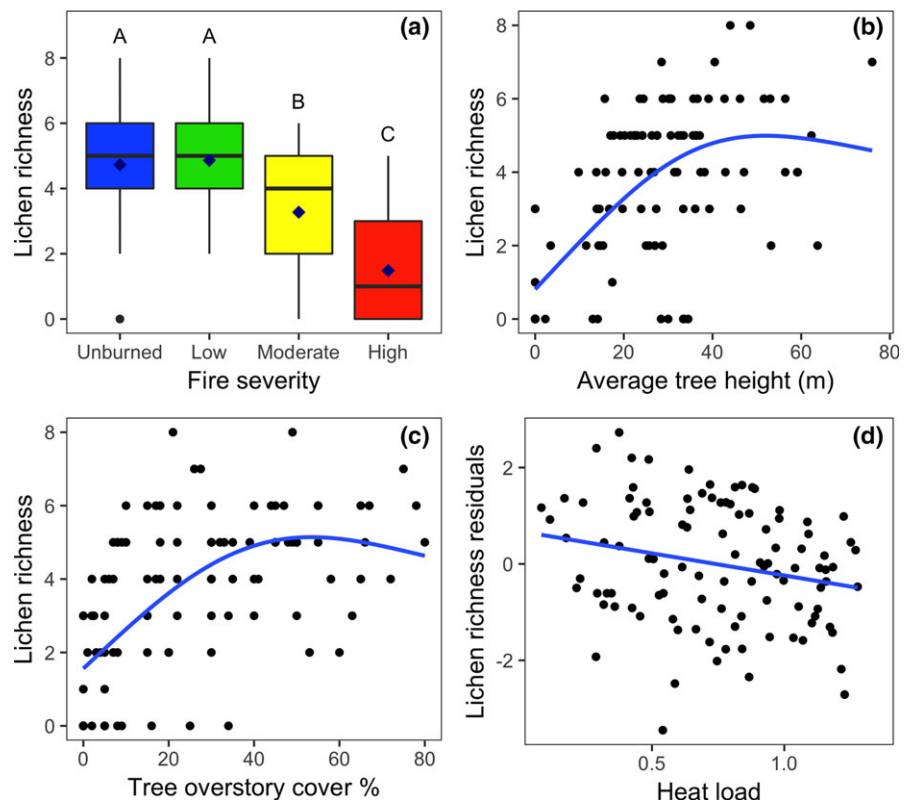
FIGURE 3 Effects of (a) fire severity, (b) average tree height, (c) tree overstory cover, and (d) topographic heat load on the lichen community. In (a), means are shown as dark blue diamonds. In (d), lichen richness residuals are from a linear mixed model that accounts for the effects of fire severity, average tree height, and tree overstory cover on lichen richness
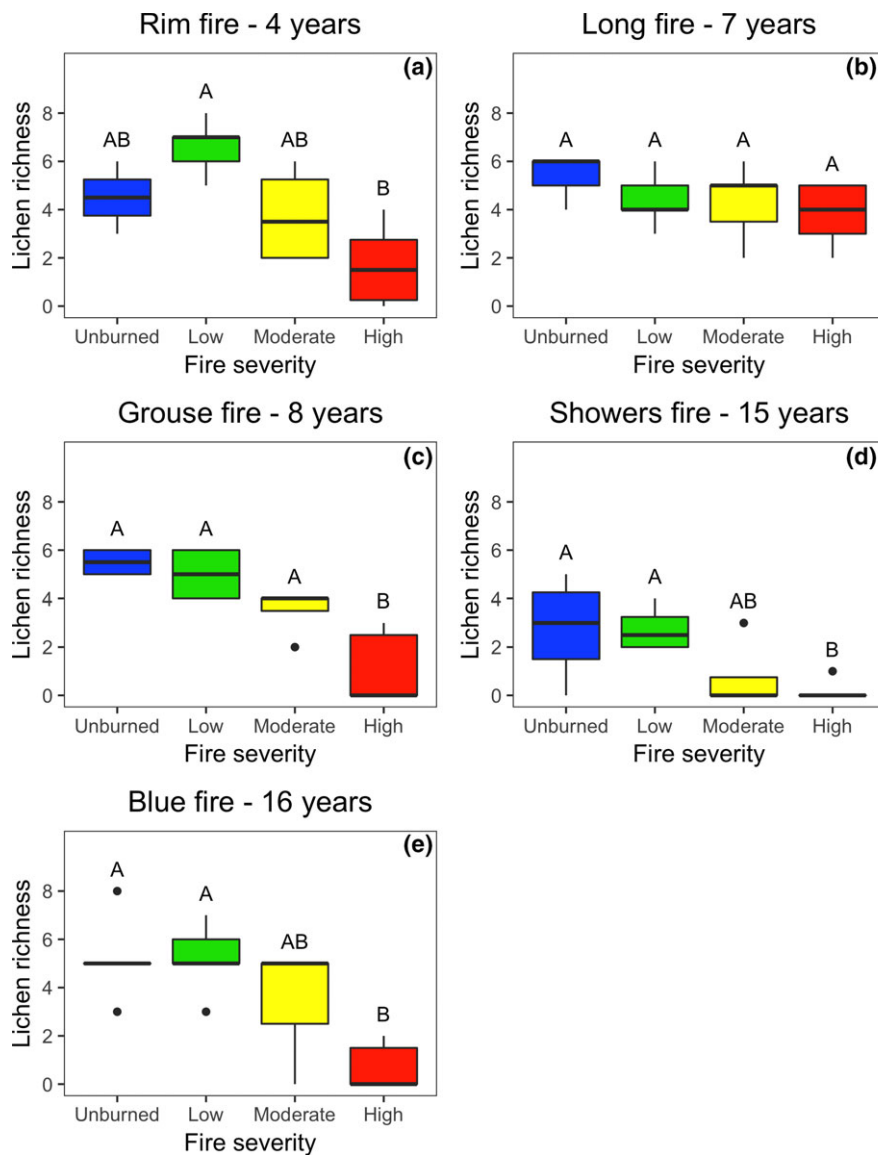
FIGURE 4 Lichen diversity responses to fire severity in the five individual fires we studied. Plots in high-severity burn areas had lower lichen richness than unburned and low-severity plots in all fires except the Long Fire (b), a managed fire that did not have any plots in the highest fire severity category (severity category 5, see Supporting Information Table S1; all fires in the high-severity category of the graph for the Long Fire are severity category 4), unlike the other four fires we studied. The difference between lichen richness in unburned and high-severity burned plots in the Rim Fire was marginally significant ($p = 0.056$)

unburned forest and areas that burned at low severity ($p = 0.99$). However, areas that burned at moderate and high severities had significantly and progressively lower richness ($p = 0.03$ and $p < 0.001$ in comparison with unburned areas, respectively). The pattern of decreased lichen richness in high-severity burn patches occurred both in the collective data set and within all individual fires, except for the Long Fire. The Long Fire was a managed fire that did not include any plots in the highest severity class (severity class 5, greater than ~90% tree mortality, Supporting Information Table S1). Across all fires, plots that burned at the highest severity (severity class 5) usually had zero lichens.

Lichen richness increased with increasing tree canopy cover ($R^2 = 0.41$, $p < 0.001$) and tree height ($R^2 = 0.37$, $p < 0.001$). There was no significant bivariate relationship between heat load and lichen richness ($p = 0.92$), although it had a significant influence on lichen richness in a multivariate model that controlled for other predictors (described below; Figure 3). Decreased lichen diversity in areas that had burned at high severity occurred

consistently across the full spectrum of fire ages we sampled—ranging from 4 to 16 years after fire—suggesting that little post-fire recolonization had taken place at any time since fire (Figure 4). In fact, lichens were only observed recolonizing burned substrates in one of the 104 plots we sampled—in an area that burned at moderate severity in the Blue Fire, the oldest fire we sampled at 16 years after fire.

Our refined structural equation model was consistent with the data (model p-value = 0.14). In this model, lichen richness was predicted by fire severity, tree canopy cover, average tree height, and heat load (Figure 5). Fire severity had both direct (though marginally significant, $p = 0.06$) and indirect effects on lichen richness; its indirect effects were mediated by tree canopy cover and average tree height. The model was consistent with our hypothesis that hotter, drier environmental conditions after high-severity fire may hinder recolonization by lichens that were present in the forest prior to the fire. The final model explained 72% of variation in lichen species richness (46% explained by fixed effects only),
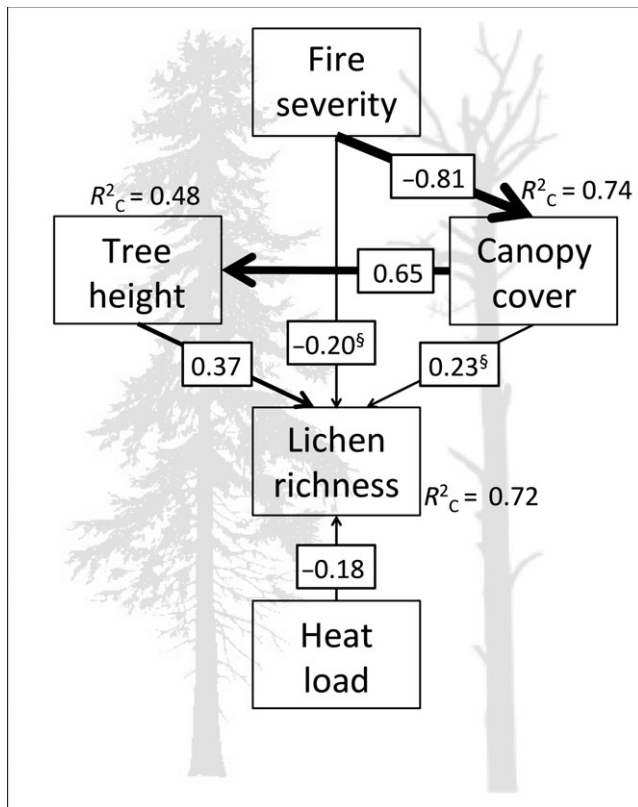
FIGURE 5 Refined structural equation model for lichen richness in postfire landscapes. Fire severity has both direct and indirect effects on lichen richness, the latter of which are mediated by tree canopy cover and average tree height. The § symbol indicates paths that are marginally significant (p = 0.06 in both cases); all other paths shown are significant (p < 0.05). Line thickness is scaled to the strength of relationships (standardized path coefficients). Conditional R^2 values (R^2_C) represent the combined explanatory power of fixed and random effects

74% of variation in tree canopy cover (68% explained by fixed effects only), and 48% of average tree height (37% explained by fixed effects only).

4 | DISCUSSION

Our findings show that altered fire regimes can have severe and long-persisting negative effects on lichen communities (Figures 3–5). The forests we studied have largely shifted from a historical fire regime characterized by frequent, low-severity fire to a contemporary fire regime characterized by infrequent fires with a large high-severity (stand-replacing) component (Agee, 1993; Safford & Stevens, 2017; Sugihara et al., 2006). Although low-severity fire—which historically typified this ecosystem—has little to no effect on lichen diversity, lichen richness drops off precipitously in areas that burned at high severity, supporting our hypothesis of decreasing lichen diversity with increasing fire severity. In fact, sites that burned at the highest severity (severity class 5), with approximately 90%–100% tree morality, usually contain no epiphytic lichens. Even more than 15 years after fire, we observe very little lichen recolonization,

despite the general availability of bark and decorticated wood substrates. While other studies have documented declines in lichen diversity after fire, initial postfire reestablishment is usually reported to occur relatively rapidly (e.g. within a few years of fire; Romagni & Gries, 1997; Mistry, 1998; Park et al., 2001). Although lichen communities may take as long as a century or more to reach late-successional community composition, this may be one of the first reports of lichens almost entirely failing to establish for >15 years after disturbance.

Altered environmental conditions and propagule limitation could explain the lack of postfire lichen recolonization that we observe. The size of high-severity burn patches in this study system has increased in recent decades (Steel et al., 2015; Steel, Koontz, & Safford, 2018), and seed limitation in the core area of these high-severity burn patches (far from living trees) is known to cause tree recruitment failure (Welch et al., 2016), suggesting that propagules of other tree-associated organisms could be limited as well. Indeed, previous research has indicated that dispersal limitation can be important in determining lichen distributions (Allen, McKenzie, Sleith, & Alter, 2017; Muir, Rambo, Kimmerer, & Keon, 2006). The symbiotic nature of lichens may make them especially sensitive to dispersal limitation, at least for species that reproduce sexually (producing fungal spores), as both the fungal and algal partners must arrive at a site for lichen establishment to occur. However, it is difficult to determine the importance of dispersal limitation without experimental manipulations. Our findings suggest that environmental changes caused by fire could limit lichen establishment in the postfire landscape, but this does not rule out the possible influence of dispersal limitation on postfire lichen community assembly.

High-severity fire appears to affect lichens both directly, by consuming them, and indirectly, by reducing canopy cover and removing tall trees that create cool, moist microclimates, supporting our hypothesis of lichen sensitivity to environmental changes caused by fire (Figure 5). It seems likely that the increased heat and solar radiation after the removal of tree canopies creates inhospitable conditions for lichens that were already living near the edge of their environmental tolerance. A similar pattern was reported by Stevens, Safford, Harrison, and Latimer (2015) for vascular plants in twelve different fires sampled in the same geographic area and forest type, where altered forest microclimate was credited with changing the relative diversities of xeric and mesic habitat specialists. As lichens appear to need the shade of tree canopies to reestablish in our study system, and altered fire regimes are causing homogeneous patterns of long-term tree regeneration failure across broad landscapes (Welch et al., 2016), our findings of long-persisting lichen diversity losses raise new concerns about the sustainability of lichen populations in fire-prone forests as fires become larger and more severe.

Our findings raise the question of whether, and when, historical forest lichen communities will reassemble in the coming decades. If forests reestablish in high-severity burn patches, it seems reasonable that suitable conditions for lichens could again occur in several-to-many decades, when tree canopies again provide buffered microclimates. However, lichen climate niches are undergoing rapid

geographic shifts due to climate change, and empirical observations suggest that lichen populations readily decline under drier, warmer conditions (Allen & Lendemer, 2016; Ellis, 2013; Nascimbene et al., 2016). In fact, there is evidence that dry, lower-elevation forests, such as those we sampled in the Sierra Nevada, contain some of the lichen communities that are most threatened by climate change in the USA (Smith, 2017). Therefore, climatic conditions that dry forest epiphytes require might not still exist in several decades when the forest potentially matures. It is conceivable that high-severity fire could catalyze long-term lichen range contractions, as climatic conditions will be substantially different in the several-to-many decades it takes for forest to reestablish. Sierra Nevada forests have long experienced some high-severity fire, but recovery of the small high-severity burn patches that occurred historically is probably a much more rapid process than recovery of landscapes where hundreds or thousands of hectares have burned in stand-replacing fire.

Forests that reestablish after disturbance but lack some previously associated organisms, such as lichens, might appear to be fully restored ecosystems at first glance. However, these cryptically degraded forests could have substantially altered function from the original forests with intact lichen communities. Because other trophic levels depend on lichens (Gerson & Seaward, 1977; Maser et al., 1985; Pettersson et al., 1995), cryptic degradation could affect invertebrates as well as avian and mammal communities. Behavior changes or range shifts in animals that eat or use lichens, such as flying squirrels (Hayward & Rosentreter, 2018) and birds (Richardson & Young, 1977), might also occur. In dry forests, pendant lichens, such as *Bryoria*, can be particularly important forage for ungulates (Richardson & Young, 1977; Marcum, 1980), and we may expect that without these resources, ungulate populations may be affected. Furthermore, nutrient cycling functions of lichens, particularly those that fix nitrogen (Denison, 1973; Nash, 2008), could be reduced. This could have negative effects on variables such as tree growth rates in forests where lichens are important nutrient sources.

Our findings highlight that interacting global change factors may cause wholesale changes in lichen communities, including lichen range contractions, which are predicted by species distribution models as well as empirical studies of lichen responses to warming conditions (Allen & Lendemer, 2016; Ellis, 2013). Although lichens may be able to recolonize after fire more rapidly in other ecosystems than they do in the semiarid forests we studied (e.g. Romagni & Gries, 2000), our findings nonetheless suggest that altered fire regimes may pose a broad threat to lichens. Beyond dry conifer forests, similar effects could be possible in any ecosystem that has experienced an increase in fire severity or frequency from historical baselines. The severity and/or frequency of burning is increasing in many parts of the world (Cochrane et al., 1999; Harvey et al., 2016; Miller et al., 2009; Prichard et al., 2017)—in part because a warmer climate causes drier fuels—and in our study system, the probability of recurrent high-severity fires is on the rise (Coppoletta, Merriam, & Collins, 2016; Safford & Stevens, 2017). While fire can maintain vegetation structure that is favorable to lichens in some ecosystems (e.g. by maintaining an open canopy structure; Mistry, 1998), high-severity fire appears to be eliminating the vegetation structure that supports lichens—such as shaded areas of bark—in the forests we studied. Our study takes place at the lower, warmer margins of many forest macrolichen distributions and may represent an early warning that similar fire-induced shifts in epiphytic lichen communities could occur elsewhere as the climate continues to warm, particularly in ecosystems where increased fire severity or fire "interval squeeze" leads to widespread deforestation and vegetation shifts (Enright et al., 2015).

Forest management practices affect fire severity, and contemporary management decisions will determine the character of currently forested landscapes for the foreseeable future. Our study highlights that maintaining tall trees, which are generally older trees, is one important management goal for maintaining lichen diversity (Figures 3 and 5). Tall trees may provide cooler, wetter microclimates than shorter trees, and old growth forests with long-lived tall trees are widely recognized to be among the best lichen habitats (Carey & Johnson, 1995; McCune, 1993; Sillett et al., 2000). Open stands of tall trees were common before Euro-American settlement in the dry conifer forests in our study area (Safford & Stevens, 2017), and recent research highlights the importance of tall trees for the spotted owl, a forest associate of conservation concern (North et al., 2017). Although wildfires are inevitable in many temperate ecosystems, open stands generally burn at lower severity than dense stands. Prefire thinning can greatly decrease tree mortality (Safford, Stevens, Merriam, Meyer, & Latimer, 2012; Strom & Fulé, 2007) and also retain some component of microclimatic conditions that favor species requiring mesic conditions, including certain groups of plants (Stevens et al., 2015) and lichens (Rambo & North, 2012). Our findings suggest that moderate stand thinning is compatible with the persistence of relatively diverse lichen communities, as postfire lichen richness in our study system peaks at ~40%–50% canopy cover, which is the target canopy cover for forest thinning in our study region (USDA, 2004). In our study system, lichen richness remains steady to slightly decreasing at >50% canopy cover (Figure 3). As high-severity fire in forests that historically burned primarily at low severity can lead to long-persisting deforested landscapes (Coppoletta et al., 2016) and reduced vegetative diversity (this paper; Stevens et al., 2015), a management focus on reducing fire severity—but not necessarily reducing fire frequency—seems a commendable goal.

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