

Epiphytic macrolichen communities take decades to recover after high-severity wildfire in chaparral shrublands

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Abstract

Aim: Fire regimes are shifting globally due to climate change, land management practices and population growth, putting species at risk if they are unable to adapt to more frequent or severe wildfires. While many fire-adapted species may be able to accommodate some amount of change in fire regimes, fire-sensitive or late-successional species that colonize fire-prone ecosystems between wildfires may be especially vulnerable to more frequent or severe fires. Here, we seek to understand the rate of lichen recolonization after high-severity fires in an ecosystem that is experiencing increasing fire frequency.

Location: The Inner North Coast Range of California, USA.

Methods: Using a chronosequence of wildfires in a Northern California chaparral shrubland, we compare lichen communities among sites that burned 3, 13, 22, 30 and 65 years previously, as well as old-growth chaparral sites without a recorded fire over the past century.

Results: We find that lichen richness increases consistently with time since fire but begins to level off 20–30 years following fire, roughly corresponding to the closure of the shrub canopy. Some taxa and guilds were found only in old-growth chaparral.

Conclusions: Our findings highlight that fire-intolerant organisms may be relatively slow to recolonize landscapes after high-severity fire and that the majority of chaparral lichen taxa may be lost where fire intervals shorten to <20 years, which has already occurred in some parts of California.

KEYWORDS

biodiversity, chaparral, chronosequence, dispersal, disturbance, fire regimes, succession

1 | INTRODUCTION

Disturbance is a key determinant of the composition of ecological communities, and fire is an especially important type of disturbance in ecosystems in Mediterranean climate zones (Keeley et al., 2012). Globally, many fire regimes (i.e. recurring patterns of fire) have shifted

towards more severe and/or more frequent fires in recent decades because of anthropogenic causes including climate change (Liu et al., 2010; Moritz et al., 2012), increased ignitions (Balch et al., 2017; Keeley & Syphard, 2019), invasive species (Fusco et al., 2019) and land management (Duren et al., 2012), including historical fire suppression (Steel et al., 2015) and outlawing of Indigenous burning

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practices (Blackburn & Anderson, 1993; Murphy et al., 2007). Shifts in fire regimes, especially when paired with the effects of climate change and invasive species, may cause substantial changes to vegetation, up to and including the type conversion of ecosystems to alternate states (Lippitt et al., 2013; Young et al., 2019). However, the effects of shifting fire regimes on biodiversity—and especially, the diversity of more cryptic organisms—remain poorly understood.

Organisms in fire-prone ecosystems typically display a range of adaptations to fire, and contemporary regional species pools have been filtered by historical fire regimes (Miller & Safford, 2020). Nonetheless, even ecosystems that have historically experienced recurring high-severity fire often contain some species that do not have adaptations to intense disturbance. Shifting fire regimes—such as increases in fire frequency or severity—could cause biodiversity losses by eliminating species without adaptations to the shorter fire-return intervals and/or more severe fires (Calabria et al., 2016; Knudsen, 2006; Knudsen & Magney, 2006). Organisms without traits that allow them to survive fires in situ will not be able to re-establish after fire unless they can disperse into burned areas. Such organisms may be particularly vulnerable to shortening fire-return intervals because they also may not have time to establish and mature before fire returns again. However, most fire ecology research has focused on vegetation structure and ecosystem type conversion, with less work examining how shifting fire regimes affect biodiversity more broadly, or post-fire dispersers specifically (Miller & Safford, 2020).

Both dispersal limitation and environmental conditions may shape the trajectories of ecological communities after fire, and substrate availability may also limit recolonization after high-severity fire. In plant communities, short-lived species with good dispersal abilities often colonize burned landscapes soon after fire (Miller & Safford, 2020; Romme et al., 2016), and the increased solar radiation that typically characterizes burned sites may also influence what species establish or persist after fire (Stevens et al., 2015). However, the relative importance of dispersal limitation and environmental conditions for shaping post-fire communities remains incompletely understood (Miller & Safford, 2020). Shortened fire-return intervals could affect both of these processes by preventing the formation of environmental conditions suitable to late-successional communities and also by decreasing time between disturbances for species to colonize and establish (Eldridge & Bradstock, 1994). Thus, shortened fire-return intervals could lead to increased dominance of early successional species and the elimination of late-successional species, potentially causing broad ecosystem state changes (Enright et al., 2015).

Lichens are a group of symbiotic organisms that have been little studied in the context of altered fire regimes, despite comprising a significant component of the biodiversity and biomass of many terrestrial ecosystems (McCune, 1993; Smith et al., 2017). Lichens play key roles in ecosystem function, such as contributing to hydrological cycles (Rundel, 1978) and soil formation (Jung et al., 2020), and providing food and habitat for wildlife (Richardson & Young, 1977). Though some lichen species are well-adapted to extreme environments, there are no known lichen adaptations to fire (Wills et al., 2018), save for early colonizing species that thrive in disturbed environments more

generally (Eversman & Horton, 2004). Even so, lichen diversity can be quite high in the later successional stages of ecosystems that experience high-severity fire, such as California chaparral (Knudsen & Kocourková, 2011; Knudsen & Magney, 2006), which is characterized by relatively infrequent, stand-replacing crown fires.

Inference into lichen responses to fire has been limited in part because most research consists of local case studies with relatively small sample sizes and/or studies that examine lichen community recovery in only the first decade or two after fire (Miller et al., 2018; Mistry, 1998; Romagni & Gries, 2000). While some research has suggested that lichens may recover relatively rapidly after fire (within a few years; Romagni & Gries, 2000), other research suggests that lichen responses to fire may be dependent on fire severity (Giordani et al., 2016). Although lichens may be little affected by low-severity fire (Pinno & Errington, 2016), recovery of lichen communities after high-severity fires may take several decades or more (Boudreault et al., 2009; Coxson & Marsh, 2001; Miller et al., 2020). If shortened fire-return intervals substantially alter lichen diversity, this could potentially cause changes in nutrient cycling, water dynamics (Stanton et al., 2014) and wildlife populations (Gustine et al., 2014; Klein, 1982).

In this study, we use a unique landscape with diverse fire histories to explore lichen community development after fire in California chaparral shrublands, an ecosystem that is experiencing shortened fire-return intervals. Lichens generally do not survive fire in chaparral, but slowly recolonize as the system recovers. We hypothesized that lichen diversity would continue to increase for several decades after fire, because we expected that some lichen taxa would not re-establish until vegetation recovered from the fire and provided suitable environmental conditions (e.g. dense canopy cover). We also hypothesized that gamma diversity (e.g. regional lichen diversity) would continue to increase with time since fire even after local diversity stabilized, since we expected that rare “old-growth” lichens might be slow to establish after fire. Finally, we hypothesized that average lichen community dispersal mode would consist of more taxa that reproduce vegetatively in the years after fire (Mistry, 1998). To test these hypotheses, we sampled lichen communities across a chronosequence of time since fire (ranging from 3 to 100+ years) in chaparral shrublands in the Northern Coast Range of California, USA. This is one of the most comprehensive studies of long-term lichen responses to fire to date.

2 | METHODS

2.1 | Study system

We studied lichen communities across a chronosequence of time since fire in chaparral shrublands in the Northern Coast Range of California. Chaparral shrublands are dominated by drought-tolerant shrubs with sclerophyllous evergreen leaves, adaptations shaped by a Mediterranean climate with dry summers and recurrent wildfires. Though the term chaparral typically refers to shrublands in

the California Floristic Province, analogous shrublands such as fynbos, maquis, matorral and kwongan occur in Mediterranean climate ecosystems around the world. Mature chaparral consists of densely packed shrubs that can support high epiphytic lichen diversity and biomass. Historical fire-return intervals in California chaparral shrublands have been estimated at 30–100+ years (Keeley & Fotheringham, 2001; West, 2003). The primary ignition source in chaparral prior to European colonization was burning by indigenous peoples such as the Wiyot, Pomo, Chumash, North Fork Mono, Konkow, Wintu, Plains Miwuk, Karuk and others (Anderson & Keeley, 2018; Keeley, 2002). These peoples regularly burned the chaparral to cultivate food and medicinal plants, for hunting and ease of travel and to reduce vulnerability to lightning-ignited wildfires. The resulting landscape is thought to have been a mosaic of chaparral, woodland and native grassland (Anderson & Keeley, 2018). Today, the primary ignition source is still humans, but these are overwhelmingly accidental ignitions from power lines and other equipment, vehicles and campfires as well as arson (Syphard & Keeley, 2015).

Many chaparral shrublands now burn more frequently than they did historically, primarily because of increased human-caused ignitions driven by population growth (Keeley & Syphard, 2019). Increases in chaparral fire frequencies are well documented in southern California, with some parts of the Santa Monica Mountains now burn multiple times in a decade (Keeley & Syphard, 2019). These frequent fires facilitate the spread of invasive grasses into chaparral systems, which in turn ignite and spread fire more easily in a “grass-fire cycle” (Zedler et al., 1983). Chaparral in Northern California has been less studied, but may be beginning to experience a similar pattern; after we completed this field study in 2018, nearly the entire study region burned again in 2020, including areas that previously burned in 2005 and 2015, representing fire intervals of just 15 and 5 years, though other surrounding areas in the study region had been long-unburned prior to the 2020 fire. Though herbaceous plants are

fairly common in the early years after fire in chaparral, over time the shrubs typically exclude fire-following annuals and the canopy closes, leaving little litter. However, if a fire occurs before the canopy closes, annual grasses may become abundant, and if fire continues to recur at short intervals, the area may convert to annual grassland (Lippitt et al., 2013; Syphard et al., 2019).

Lichen communities of chaparral shrublands in California have been documented since the late 1800s (Hasse, 1898; Knudsen & Magney, 2006), and shortened fire-return intervals may be reducing landscape-scale lichen diversity. Resurveys of areas studied by Hasse in the 2000s found that many previously documented lichen species had been extirpated and that some lichen species were restricted to “old-growth” chaparral stands that had not burned in over a century (Knudsen, 2006; Knudsen & Kocourková, 2008; Knudsen & Magney, 2006). However, these studies did not include a quantitative examination of the effects of site fire histories on lichen diversity. Lichen re-establishment after fire in chaparral may be limited by the presence of suitable substrates (e.g. woody substrates may have to regrow before epiphytic lichens can establish, though some pioneer lichens will begin by colonizing charred stems or other remains); dispersal limitation and altered environmental conditions after fire may also influence post-fire community assembly (Johansson, 2008; Wills et al., 2018).

To test how time since fire shapes lichen communities, we sampled lichen communities at the Quail Ridge Natural Reserve and the nearby Stebbins Cold Canyon Reserve in Napa and Solano Counties, California in February 2018 (Figure 1). We used records from CAL FIRE's Fire Resource and Assessment Program (FRAP) and Quail Ridge Reserve records to identify the boundaries of fires that had occurred within the reserves since 1950. We selected five fires to sample: the 1953 T. View Fire (134 ha), the 1988 Resort Fire (195 ha), the 2005 Pleasure Fire (106 ha), an unnamed 1996 fire (~4 ha) and the 2015 Wragg Fire (3,258 ha). Most of the area that burned in the 1988 fire had previously burned in the 1952 Cliff Meagher fire (not

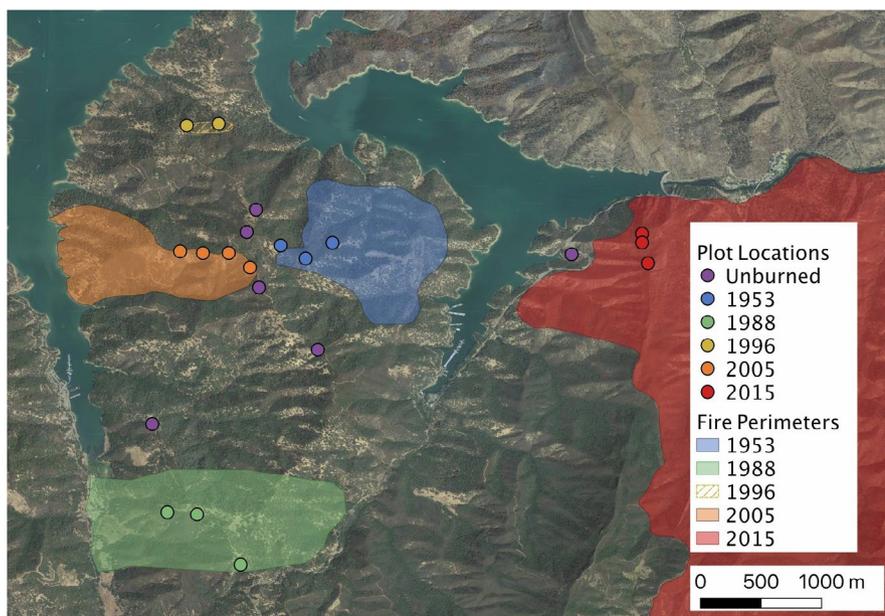


FIGURE 1 Map of study sites at the UC Davis Quail Ridge and Stebbins Cold Canyons Reserves in Napa and Solano Counties, California. Dashed lines on the 1996 fire indicate an estimated fire perimeter. Only the most recent fire (as of 2018) that burned the locations of the study plots is shown; most of the area that burned in the 1988 fire had also burned in 1952, and all of the area burned in 2015 burned previously in 1988

shown on the map), and all of the area burned in 2015 had previously burned in the 1988 Miller Fire (not shown on the map). As most fires in this area are high-severity and stand-replacing, we only consider the most recent fires in our study plot locations in the analysis.

All of our study sites occurred in chaparral where shrubs are the most abundant vegetation (or were prior to fire; in recently burned areas standing dead shrubs were present). Our study plots were dominated by chamise (*Adenostoma fasciculatum*, which made up at least 50% of shrub cover in all plots); *Ceanothus* species, toyon (*Heteromeles arbutifolia*), manzanita (*Arctostaphylos* sp.) and scrub oak (*Quercus berberidifolia*) were also common. These evergreen shrubs all exhibit adaptations to a historical high-severity fire regime, such as resprouting and/or fire-cued seed germination. We observed that chamise seems to be an excellent lichen substrate; it generally hosts more diverse communities than other co-occurring shrubs J. E. D. Miller, A. Weill, and J. Villella (personal observations, February 2018). The study site is situated on the edge of the area influenced by summer coastal fog (Torregrosa et al., 2016), and this source of moisture likely influences the composition of the macrolichen community (Stanton & Horn, 2013; Wirth et al., 2010).

2.2 | Data collection

In each burn area, we arbitrarily selected 2–4 study plot locations in chaparral vegetation on southeast- to southwest-facing slopes by placing points on a map prior to fieldwork. We established three plots in the 2015 fire, four plots in the 2005 fire, two plots in the 1996 fire, three plots in the 1988 fire and three plots in the 1953 fire. For each fire, we also selected one or two study plot locations that were unburned in recorded fire history outside of the fire perimeter, for a total of six unburned study plots (except for the 1996 fire, where we did not encounter suitable adjacent unburned habitat). Thus, we sampled a total of 21 plots across the six different fire history categories.

To sample lichen communities, we used a modified (smaller) version of the Forest Inventory and Analysis off-grid study plot protocol: circular plots with a 4.37 m radius (following Welch et al., 2016). In each plot, we searched the plot for epiphytic macrolichens and recorded all lichen taxa encountered growing on stems and branches. We collected any lichens that could not be identified in the field for further identification in the laboratory. We estimated shrub cover in each plot (as if viewing the plot from above), and we also recorded slope and aspect, to assess whether topographic heat load had a confounding effect on lichen communities. Topographic heat load is an adjusted version of solar radiation that attempts to account for west-facing slopes being warmer than east-facing slopes; it is calculated from latitude, aspect and slope (McCune & Keon, 2002).

We identified lichens using McCune & Geiser (2009), Nash (2002), an unpublished regional key (personal communication, Tom Carlberg) and an unpublished key to North American Physciaceae (personal communication, Ted Esslinger). Nomenclature follows (Esslinger, 2019), except for the recently described *Physcia*

rhizinata (Esslinger et al., 2020) and a distinctive *Usnea* morpho-species that could not be identified ("*Usnea* sp. 1", personal communication, Trevor Goward).

To test whether community-level dispersal mode changed with time since fire, we used the literature to assign all taxa as either reproducing vegetatively or not (following Mistry, 1998). To explore whether lichen functional groups recovered from fire at different rates, we assigned taxa to four functional groups: minute foliose chlorolichens (Physcioid lichens, *Polycauliona* and *Candelaria*), large foliose chlorolichens (all other foliose lichens with green algal photobionts including *Hypogymnia*), fruticose lichens and cyanolichens.

2.3 | Statistical analyses

To explore drivers of the recovery of lichen richness after fire, we used a linear mixed-effects model with local lichen richness as the response variable and time since fire, shrub cover and heat load as predictor variables. Because plots within each fire were spatially clustered, along with an unburned plot just outside the fire perimeter for most fires, we included fire block as a random effect. Each fire block included all the plots sampled from the same fire as well as any adjacent unburned plots. Because the resulting model had a singular fit, we then reran the model as a simple linear model with block as a fixed effect rather than a random effect to increase statistical power. Because fire block was not significant in the resulting model, we removed the block term and reran the model.

To test whether lichen richness, shrub cover and the proportion of taxa reproducing vegetatively varied among different time since fire classes, we used simple ANOVA with Tukey post hoc tests. Because sample sizes varied among different time since fire categories, we calculated Chao estimated richness to represent gamma diversity within each time since fire category using the vegan package (Oksanen et al., 2019). To explore whether lichen species composition varied with time since fire, we performed a PERMANOVA test with time since fire and shrub cover as predictor variables; this was performed with 999 permutations using Bray–Curtis dissimilarity with the vegan package. We visualized species composition using non-metric multidimensional scaling; a two-dimensional solution using Bray–Curtis dissimilarity with stress of 0.094 is presented.

3 | RESULTS

Plot-level lichen richness was very low three years after fire (mean = 2.3 taxa per 60-m² plot, and one site contained no lichens whatsoever), but it increased steadily in the following decades. Mean lichen richness was 7.3 taxa 13 years after fire and 14.5 taxa 22 years after fire. Local lichen richness began to level off after the 22-year-old fire, with only a non-significant increasing trend past that point, eventually reaching a mean richness of 18 taxa in long-unburned plots (Figure 2a). Gamma diversity (estimated Chao richness) within each fire history class continued to increase with

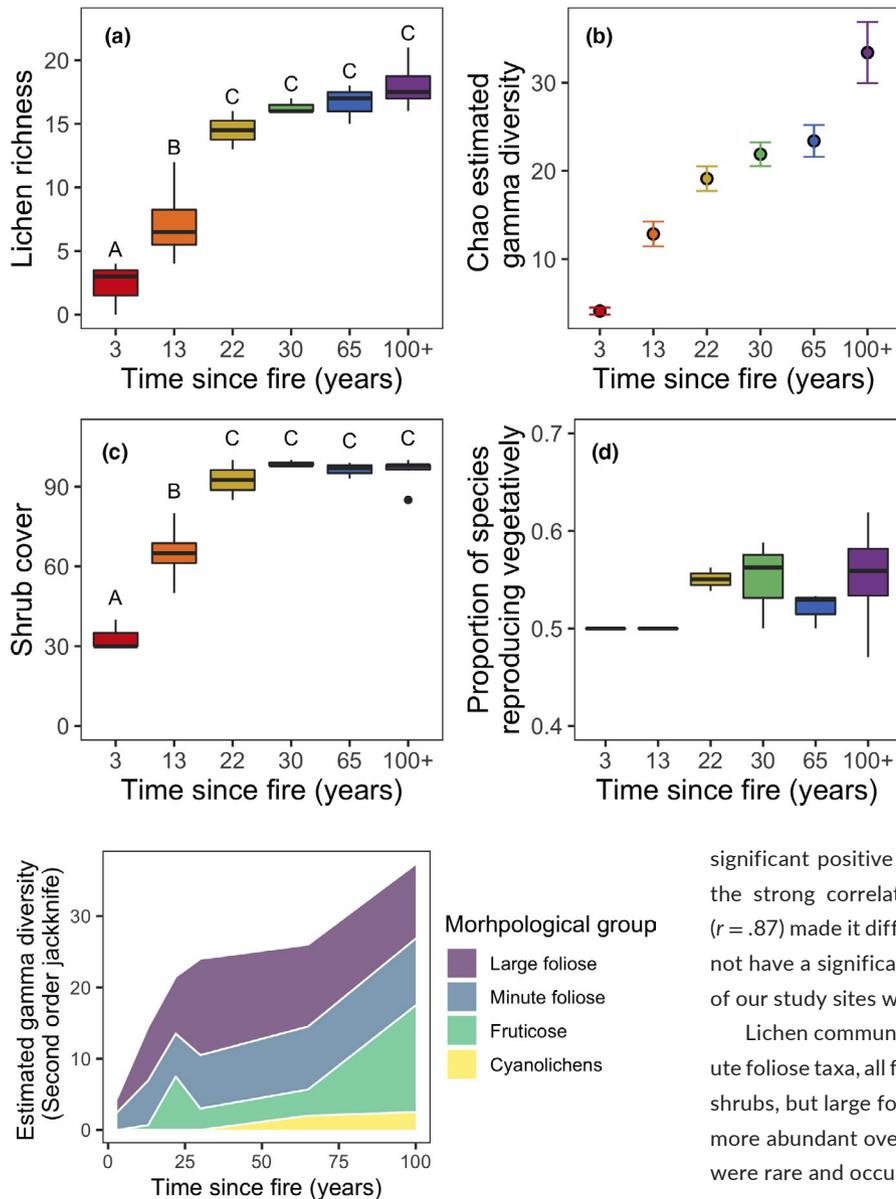


FIGURE 3 Change in the landscape-level richness of macrolichen morphological groups with increasing time since fire. Minute foliose lichens are the earliest colonizers after fire, with large foliose and fruticose taxa becoming more abundant decades later, and cyanolichens appearing last. Minute foliose lichens are defined as *Physcia*, *Physconia*, *Candelaria* and *Polycauliona* spp. All other foliose lichens including *Hypogymnia* are considered large foliose lichens

time since fire, breaking 30 taxa only at long-unburned (100+ years since fire) plots (Figure 2b). The proportion of taxa reproducing vegetatively did not change significantly with increasing time since fire ($p = .284$; Figure 2d). Taxa that were present in each time since fire class are shown in Table S1.

The response of local lichen richness to time since fire mirrored the response of shrub cover, which reached 90% 22 years after fire and then levelled off (Figure 2c). The linear model for local lichen richness indicated that both time since fire and shrub cover had a

FIGURE 2 Relationships between time since fire and (a) plot-level lichen species richness, (b) estimated gamma diversity (regional lichen richness based on the Chao estimator) within each time since fire category, (c) percent cover of shrubs at the plot level and (d) the proportion of taxa reproducing vegetatively at the plot level. Letters above boxes in (a) and (c) represent results of Tukey post hoc tests

significant positive influence on lichen richness (Table S2), though the strong correlation between time since fire and shrub cover ($r = .87$) made it difficult to disentangle their influence. Heat load did not have a significant effect on lichen richness, perhaps because all of our study sites were on relatively warm slopes (Table S2).

Lichen communities 3 years after fire consisted primarily of minute foliose taxa, all found growing on the charred, dead stems of large shrubs, but large foliose and fruticose lichens became progressively more abundant over the following decades (Figure 3). Cyanolichens were rare and occurred only in the densely shaded chaparral understory of well-developed stands that had not burned for 65 years or longer. Of the 37 total lichen taxa we observed in this study, eight occurred only in the long-unburned chaparral stands, and 18 occurred only in stands that had been unburned for 30+ years.

The PERMANOVA indicated that both time since fire ($R^2 = .401$, $p = .001$) and shrub cover ($R^2 = 0.16$, $p = .004$) had significant effects on lichen species composition (Figure 4).

4 | DISCUSSION

Our findings highlight that fire-intolerant organisms may be relatively slow to recolonize landscapes after high-severity fire. Local lichen richness increased until 22 years after fire, but gamma diversity continued to increase throughout the study period, and some taxa and guilds appeared to be restricted to only long-unburned chaparral. For example, we did not observe cyanolichens in areas burned more recently than 65 years before the study. These findings suggest that increasing fire frequencies could cause substantial

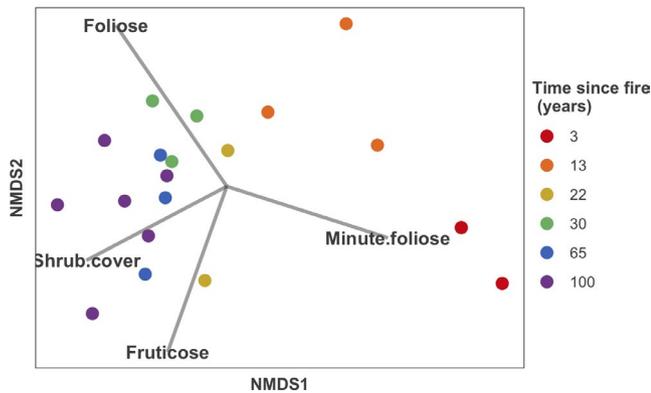


FIGURE 4 An ordination illustrates that lichen communities shift incrementally towards “old growth” chaparral lichen communities with increasing time since fire (PERMANOVA $p = .001$ for effect of time since fire on species composition). One of the plots from three years after fire is not shown because no lichen species were present

lichen biodiversity losses in chaparral shrublands. Late-successional lichens could be entirely eliminated from the landscape even with modest increases in fire frequency, aligning with previous predictions of extreme ecosystem changes caused by increasing fire frequency (Enright et al., 2015). More extreme shortening of fire-return intervals (e.g. intervals below 20 years) could greatly reduce landscape-scale lichen diversity of common “matrix” lichens as well. As extreme interval squeeze may eventually convert chaparral shrublands to grasslands (Zedler et al., 1983), epiphytic lichens could even be entirely eliminated from the landscape under highly altered fire regimes.

Both dispersal limitation and altered environmental conditions after fires may limit lichen recolonization after fire (Miller et al., 2020). Although dispersal limitation is known to be an important determinant of lichen distributions (Allen et al., 2017; Armstrong, 1990; Ellis, 2012), we found that average lichen community dispersal mode did not change significantly with time since fire as we had hypothesized. This finding contrasts with previous findings that lichens that reproduce vegetatively may recolonize more quickly after fire (Eversman & Horton, 2004; Mistry, 1998), and suggests that propagule availability might not be the primary limiting factor of lichen recolonization after fire in this ecosystem. Our study sites were often placed at accessible sites close to the edges of fire perimeters, so dispersal limitation could be stronger in other locations on the burned landscapes farther from propagule sources. Experimental tests would be needed to fully tease apart the relative importance of dispersal and establishment limitation in post-fire lichen recolonization. Further work could also investigate other groups of lichens; saxicolous lichens are likely less sensitive to fire than epiphytes (Koch et al., 2015), while epiphytic microlichens might show similar responses to the epiphytic macrolichens we document here.

Nonetheless, substrate availability is clearly an important limitation for lichen community development, and environmental

conditions in the post-fire landscape appear to be important for lichen recolonization as well. We observe that lichen richness after fire increases most rapidly around the time when large, continuous shrub canopies develop, suggesting that the development of shaded microclimates may both be important for community assembly. The development of a greater quantity and diversity of substrates at this point in development likely plays a role; the earliest post-fire epiphytic lichen growth was limited to charred, dead shrub stems. Lichens are known to be sensitive to environmental conditions given their poikilohydric nature, and species composition is shaped by aridity in dry Mediterranean environments (Matos et al., 2015). Changes to microclimates have been identified as a driver of lichen community change following disturbance (Johansson, 2008; Kantvilas & Jarman, 2006), with high irradiance, wind exposure and evaporation rates common to recently disturbed environments. The role of microclimates in our system is illustrated by the dominance of shade-intolerant pioneer genera such as *Polycauliona* in the early years after fire; in older stands, these genera were largely limited to shrub branch tips exposed to sunlight at the top or edge of the canopy (personal observations).

While many plants in ecosystems characterized by recurring high-severity fire have adaptations that allow them to survive or rapidly re-establish following fire, the persistence of other fire-sensitive taxa such as lichens likely depends on long fire intervals to allow time for recolonization and/or the development of suitable environmental conditions. Very short fire-return intervals may also prevent the persistence of even fire-adapted plant species, such as chaparral shrubs that need time between fires to build up a seed bank (Margolis et al., 2020; Tyler & Odion, 2020), potentially eliminating foundation species that lichens or other epiphytes use as a substrate. Other fire-sensitive species such as vertebrate and invertebrate animals with limited adaptations to fire may also decline with the global trend towards larger, hotter fires (Engstrom & Todd Engstrom, 2010; Wintle et al., 2020). For some late-successional species, lichens themselves may provide habitat (Pettersson et al., 1995); in forested ecosystems, lichens are known to be important food sources for old-growth forest-associated vertebrates (Asplund & Wardle, 2017; Rosentreter et al., 1997). Thus, the development of cryptic organisms such as lichens after fire may provide a foundation for the further development of late-successional communities. As fire-intolerant organisms generally must recolonize from outside burned areas (Wills et al., 2018), these findings suggest that increasing size of global wildfires could interact with increasing fire severity to reduce post-fire diversity for organisms in many fire-sensitive taxonomic groups.

The conservation value of late-successional or old-growth forests has long been recognized, but the conservation value of late-successional grasslands, shrublands and savannas has historically received less attention (Veldman et al., 2015). This is beginning to change with the recent emergence of the “old growth grasslands” and “old growth chaparral” concepts (Knudsen & Kocourková, 2008; Veldman et al., 2015) and the growing recognition that “conservative” species that are averse to disturbance occur in many

ecosystems (Bauer et al., 2018). Our study demonstrates that even in non-forested habitats, long-unburned, "old growth" vegetation may promote biodiversity, even though it is often unrecognized. In our study system, this emerging paradigm contrasts with the historical dismissal of chaparral shrublands as overgrown brush that poses a fire hazard (Rundel, 2018). Our study also highlights that documenting the diversity of cryptic organisms such as lichens remains a work in progress; *Physcia rhizinata*, one of the most common lichen species we encountered in our study area, was described recently based on a type specimen from a population we discovered in the course of this study (Esslinger et al., 2020).

4.1 | Management implications

Managing chaparral and other Mediterranean shrublands for wildfire risk, biodiversity and cultural value can be a particular challenge. The proximity of these ecosystems to major population centres and their propensity for large, intense wildfires that often burn under severe fire weather conditions necessitates making management for wildfire risk a priority (Rundel, 2018). Strategies that focus on removing fuel such as prescribed burning or mastication should be used judiciously in chaparral and similar systems (Busby & Southworth, 2014; Duren & Muir, 2010), given the risk of biodiversity loss and type conversion when fires occur at short intervals. Some authors suggest prioritizing the prevention of human ignitions, development planning and structure protection over regional vegetation management for chaparral ecosystems, especially in the light of the presence of flammable non-native grasses (Anderson & Keeley, 2018; Keeley & Syphard, 2019). However, when paired with prevention and home protection efforts, a land management strategy that aims for a well-maintained mosaic of land types, including some areas of old-growth chaparral as well as more open, savanna-like areas that are managed with prescribed fire, could potentially serve to reduce fire risk and maximize cultural and ecological value (Airey Lauvaux et al., 2016).

A well-planned combination of management strategies could protect old-growth chaparral sites and the biodiversity therein even as fires become larger and more frequent, particularly if these strategies are applied in a heterogeneous fashion that leaves some old-growth chaparral stands unburned while reducing the risk of damaging wildfire. The best approach to protect lichens in chaparral and other systems adapted to high-severity fire will be different from what is appropriate in other ecosystem types (Keeley & Syphard, 2019). For example, the reintroduction of frequent fire is appropriate in low-elevation forests and woodlands in California that historically burned in frequent, low-severity ground fires; such fires generally have positive effects on biodiversity in general (Miller & Safford, 2020) and have relatively little impact on lichens growing in the forest canopy (Miller et al., 2018). In contrast, chaparral shrublands typically burn at high severity, limiting lichen community assembly to periods between fires; thus, chaparral is likely to be more sensitive to increasing fire frequency than other adjacent ecosystems. Our findings highlight the importance of considering

the unique historical fire regimes of different ecosystems in the development of management strategies.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.pzgmsbckp>.

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BIOSKETCH

The authors are interested in the effects of global change processes on biodiversity, and cryptic organisms in particular.

Author Contributions: AW and JM designed the study, all authors conducted fieldwork and laboratory work, JM analysed the data, JM and AW wrote the first draft of the manuscript, and all authors edited the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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