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ARTICLE

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The effects of a half century of warming and fire exclusion on montane forests of the Klamath Mountains, California, USA

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Abstract

Climate warming and altered disturbance regimes are changing forest composition and structure worldwide. Given that species often exhibit individualistic responses to change, making predictions about the cumulative effects of multiple stressors across environmental gradients is challenging, especially in diverse communities. For example, warming temperatures are predicted to drive species upslope, whereas fire exclusion promotes the expansion of species at lower elevations where fire was historically frequent. We resampled 148 vegetation plots to assess 46 years (1969–2015) of species and community-level response to warming and fire exclusion in a topographically complex landscape in the Klamath Mountains, California, USA, a diverse region that served as a climate refugia throughout the Holocene. We compared cover and assessed change in the elevational distributions of 12 conifer species at different life stages (i.e., seedlings, saplings, canopy). We observed consistent but non-significant shifts upward in elevation for eight species, and a significant shift upward for one species, all of which were far less than expectations based on recent warming. Six species declined in total cover and another five declined in at least one life stage, whereas the drought- and fire-intolerant *Abies concolor* increased by 30.7%. The largest declines were at lower elevations in drought-tolerant, early-seral species (*Pinus lambertiana* and *Pinus ponderosa*) and at higher elevations for the shade-tolerant *Abies magnifica* var. *shastensis* and the regionally rare *Abies lasiocarpa*. Regionally rare (*Picea engelmannii*) and endemic (*Picea breweriana*) species had reductions in early life stages, portending future declines. Multivariate analyses revealed a high degree of inertia with a minor, but significant, shift in composition and a slight decrease in species turnover along the elevation gradient driven by the expansion of *A. concolor*. Our results indicate that most species are declining, especially at lower and mid-elevations where fire exclusion has increased the cover of shade-tolerant species and reduced the recruitment for fire-adapted species. Collectively, declines in most species, insufficient upward movement to track warming, reductions in drought- and fire-tolerant early-seral species, and an increase in a single, shade-tolerant species will leave these communities maladapted to projected climate scenarios and questions the potential for future climate refugia in this region.

KEYWORDS
beta-diversity, climate change, climate refugia, fire exclusion, Klamath Mountains, legacy plots, non-parametric multiplicative regression, tree mortality

INTRODUCTION

Forests are experiencing marked changes worldwide in response to a warming climate (Allen et al., 2015; Das et al., 2013; McDowell et al., 2018), legacies of past land management (Collins et al., 2017; Dolanc, Safford, Thorne, & Dobrowski, 2014; Gilliam & Platt, 1999; Li & Waller, 2017), and increases in insect and pathogen outbreaks (Aukema et al., 2010; Weed et al., 2013). These novel stressors interact and affect key tree demographic processes such as growth, recruitment, and mortality (McDowell et al., 2020), thereby shifting species distributions and patterns of forest community composition and structure at stand and landscape scales. However, predicting community-level effects from local population change is difficult, as species have responded individualistically to past climate change (Briles et al., 2005, 2011; Daniels et al., 2005; Mohr et al., 2000; Whitlock et al., 2003). Furthermore, species responses may be mediated by both the interactions among stressors (DeSiervo et al., 2018; Monleon & Lintz, 2015; Wason & Dovciak, 2017) and complex topography that may offer refugia from warming (Ackerly et al., 2020; Bost et al., 2019; Wason et al., 2017). For forested communities, an understanding of species-specific responses will be necessary for predicting community and landscape change arising from multiple anthropogenic drivers of change (Socolar et al., 2016).

Climate is one of the most important determinants of species range distributions (Whittaker, 1960). Therefore, one observed impact of rising temperatures on global tree distributions is the poleward or upward movement in elevation, such that species spatially track their climate niche (Aitken et al., 2008; Beckage et al., 2008; Lenoir et al., 2008). In addition, other studies have demonstrated that the timing, magnitude or even the direction of elevation shifts in vegetation do not always track expectations based on recent warming (Bertrand et al., 2011; Harsch et al., 2009; Masek, 2001; Savage & Vellend, 2015). These studies and others document a time lag in the biotic response of tree species to recent environmental change by comparing the observed magnitude of change (for example, migration rate or shifts in plant cover) to the expected magnitude of change predicted by shifts in climate (Savage & Vellend, 2015). Some proposed explanations for this lag include low seed production, barriers to dispersal, poor soil conditions (Aitken et al., 2008; Masek, 2001), or interactions with other organisms (Kaarlejärvi & Olofsson, 2014).

Concurrent with rapid climate change, many tree communities in western North America are responding to legacies of 20th century land management, most notably, the exclusion of historically frequent fire. Impacts of fire exclusion in western North America include stand homogenization and the loss of canopy gaps (Lydersen et al., 2013) due to increases in shade-tolerant, fire-sensitive conifers such as *Abies* spp. (firs) (Dolanc et al., 2013; Johnston, 2017; Minnich et al., 1995; Vankat, 2011). Increased stand density and competition decrease growth in mature and old trees, potentially predisposing them to drought-induced mortality or increasing their susceptibility to pathogens and insects (Allen et al., 2015; Meddens et al., 2015). Fire exclusion and increased density also reduce recruitment of fire-adapted, early-seral species (i.e., *Pinus* spp., pines) and may leave communities maladapted to future climate conditions and disturbance (Serra-Diaz et al., 2018).

The combination of warming temperatures and fire exclusion results in forests in the modern era contending with a unique set of stressors with no historical analog (Millar et al., 2007). In previous periods in Earth's history when temperatures were warming, there was also increased fire activity across forested landscapes (Briles et al., 2005; Mohr et al., 2000). More recently, tree communities in western North America have experienced a combination of frequent and extreme droughts along with a century of fire exclusion and long-term fuel accumulation, further increasing forest susceptibility to high-severity fire (Adams et al., 2009; Allen et al., 2015; Allen & Breshears, 1998; Kane et al., 2014). Other impacts of the interaction of multiple anthropogenic drivers of change may be more subtle, producing shifts in abundance that are less extreme than if only one change was occurring. For example, warming temperatures are predicted to drive species upslope, whereas the absence of disturbance might promote the expansion of shade-tolerant taxa that limit canopy gaps needed for recruitment, including recruitment into new positions above range margins. The novel interaction of multiple anthropogenic drivers of change in the 21st century prompts the need for more studies that evaluate recent changes in vegetation composition.

Repeat sampling of "legacy plots"—plots established by earlier ecologists decades ago that are spatially referenced and include documented sampling methods (Stuble et al., 2021; Vellend et al., 2013)—provide important observations of long-term changes in tree distributions (McIntyre et al., 2015; van Mantgem et al., 2009) and community composition and structure (Dolanc, Safford, Thorne, & Dobrowski, 2014; Rogers et al., 2008; Savage & Vellend, 2015). A unique feature of studies that resample legacy plots is their emphasis on natural history, yielding detailed, fine-scale community composition data on a decadal time scale (Vellend et al., 2013); these data are not available from other common methods of assessing long-term vegetation change such as paleoecology and remote sensing. However, legacy plot studies are subject to inherent limitations depending on their methods, documentation, and whether plots were permanently monumented in such a way that they can be located precisely. Although the existing literature indicates that long-term legacy plot studies are robust to uncertainty in location and methodology, understanding these and other limitations is crucial to the interpretation of change (Kopecký & Macek, 2015; Vellend et al., 2013).

Among other valuable information, legacy studies are useful for documenting recent, sometimes subtle, changes in community composition, including elevation shifts. For example, Savage and Vellend (2015) showed that tree species in southern Quebec, Canada moved upward an average of 27.4 m over a 40-year period using historical plots (6.85 m per decade). Also, Kelly and Goulden (2008) showed that several tree species had moved upward an average of 57 m between 1977 and 2006/2007 in Southern California, USA. Most studies that document long-term shifts in forest community composition have been conducted in regions where overall tree diversity is relatively low (e.g., HilleRisLambers et al., 2015; McIntyre et al., 2015), therefore the trajectory of less common and rare tree species and the cumulative effects on community composition, beta-diversity, and landscape heterogeneity remain unclear.

We report on a comparison of 146 legacy plots sampled in 1969 and 2015 in the Russian Wilderness, a federally designated wilderness in the central Klamath Mountains (Figure 1). Most of the Russian Wilderness are has not experienced a fire in more than a century (Safford et al., 2011), therefore this study area exemplifies much of the fire-excluded landscape of the region. The initial 1969 sampling was completed by John Sawyer and Dale Thornburgh, two professors at Humboldt State University (California, USA), and focused on describing plant associations along topographic gradients (Sawyer & Keeler-Wolf, 1995; Sawyer & Thornburgh, 1974). Their study was the first to formally document what is now considered the highest density of conifer species in the world, with 18 conifer species in a 2.6 km^2 area known locally as the "Miracle Mile" (Kauffmann, 2012; Table 1). Sawyer and Thornburgh (1974) largely focused their sampling efforts within the montane and subalpine zones (>1650 m elevation). Recent modeling studies have suggested lagged responses to climate change in this region (Serra-Diaz et al., 2018) and indicated that these zones may be particularly vulnerable to change due to increasing temperatures and reduced winter snowpack (Garwood et al., 2020; Maxwell & Scheller, 2020). Despite many paleoecological studies of the Klamath Mountains, there are no long-term assessments of recent changes in upper-montane trees communities to compare with projected future changes.

Our primary objectives were to assess changes in the abundance and distribution of a diverse assemblage of conifer species in the Russian Wilderness from 1969 to 2015 and to compare how individual species with differing life histories and traits (i.e., drought, fire, and shade tolerance; Table 1) respond to multiple stressors (i.e., climate warming and fire exclusion). We then assessed the emergent effects of species-level responses on patterns of community change and compared these patterns with events in similar landscapes affected by climate change and fire exclusion. Although projections of forest community change in the diverse landscapes of northwestern California are available from modeling studies (Maxwell & Scheller, 2020; Serra-Diaz et al., 2018; Thorne et al., 2020), our work is the first to document change in the Klamath Mountains using observations from a long-term study.

We made separate predictions for three categories of conifers based on species life history traits (Table 1), paleoecological studies in nearby (~50 km) high-elevation landscapes (please refer to Briles et al., 2011), and recent decadal-scale studies of forest change in mountainous landscapes dominated by coniferous forests of the western United States (Dolanc et al., 2013; Minnich et al., 1995). First, for shade-tolerant, fire-intolerant species, we predicted expansion due to fire exclusion, but contraction at lower elevations due to recent warming. Second, for high-elevation species near their southern range limits, we predicted declines in abundance in warmer and lower elevation sites, increases in abundance in cooler and higher elevations, and stability in topographically sheltered landscape settings offering refugia from climate change. Third, we predicted that fire-tolerant, shade-intolerant species would decline due to fire exclusion and the loss of canopy gaps at lower elevations where fire was historically the most frequent, but would expand upward due to climate warming.

METHODS

Study landscape

The Klamath Mountains of Northern California and southwestern Oregon harbor some of the most diverse plant communities in North America (Figure 1; Coleman & Kruckeberg, 1999; Whittaker, 1960). Plant assemblages in the region vary considerably over short distances with high levels of beta-diversity, in part because of the geological variation, steep elevation gradients, and complex topography (Sawyer, 2007; Whittaker, 1960). Our study was

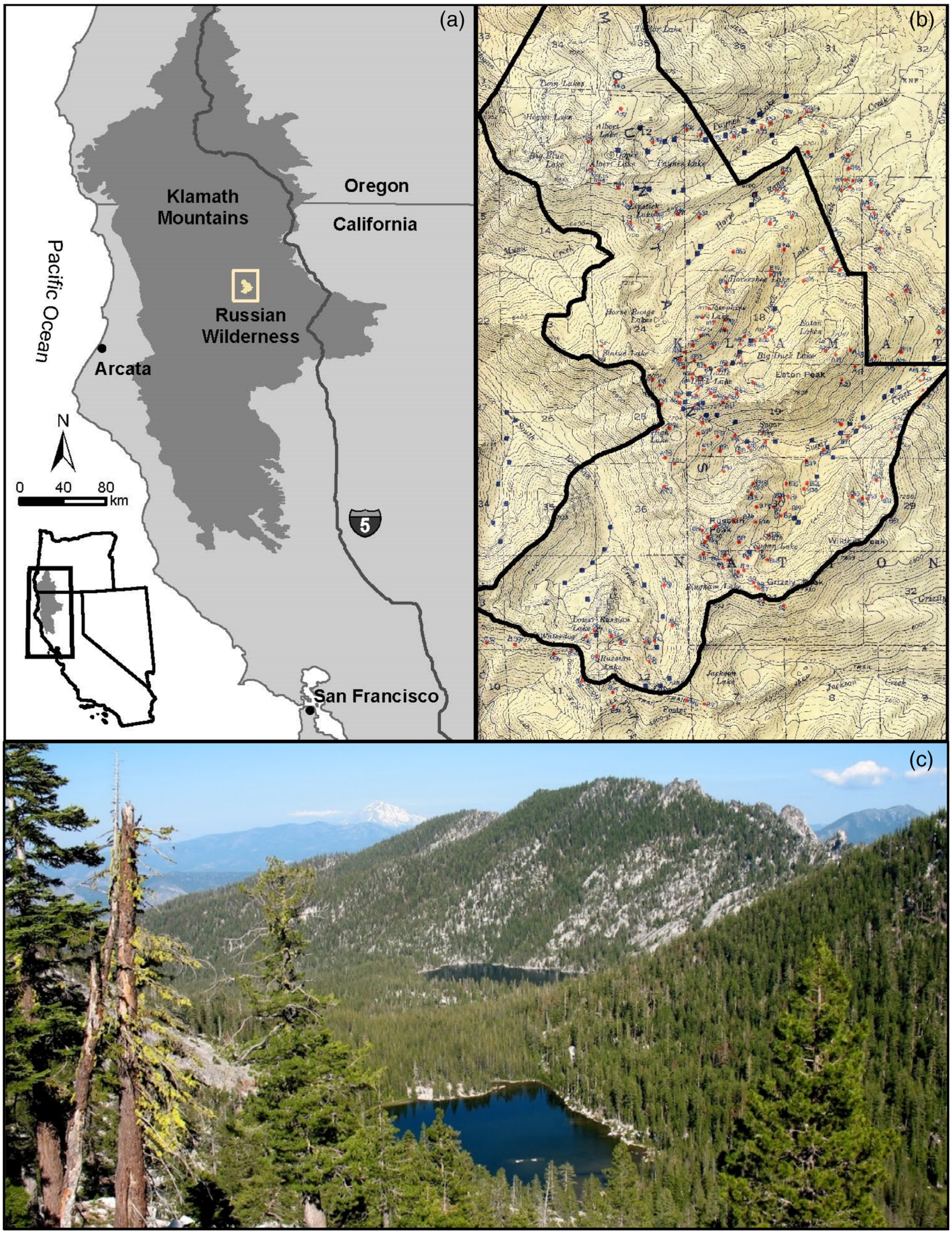

FIGURE 1 The study area where the abundance of tree species was recorded in a 1969 study and a resurvey of the same plots in 2015 in the Klamath Mountains of California, USA. Panel (a) shows the Klamath Mountain region and the Russian Wilderness study area highlighted with the rectangle. Panel (b) shows the original map of the study area with red points hand-drawn in 1969 by John Sawyer and Dale Thornburgh indicating plots locations. An example of the data sheets associated with each plot is shown in Appendix S1: Figure S2. Panel (c) shows a portion of the study area; the lake in the foreground, Little Duck Lake, is at 2030 m elevation, and the ridge in the upper portion of the photograph, Eaton Peak, is at 2328 m. Plots in the study ranged from 1300 m to 2469 m. Mt. Shasta (4322 m) is the snow-covered peak in the background and is found in the adjacent Cascade Mountains. Photograph by M.E. Kauffmann.

TABLE 1 Twelve conifer species that were observed in a 1969 study and a resurvey of the same plots in 2015 in the Klamath Mountains of California, USA.

Species	Shade tolerance	Drought tolerance	Fire strategy	Range	Fire exclusion abundance prediction	Climate change abundance prediction
Abies concolor	Tolerant	Intolerant	Avoider	Widespread	Expansion	Decline
Abies lasiocarpa	Tolerant	Intolerant	Avoider	Southern limit	Expansion	Decline
Abies magnifica var. *shastensis*	Tolerant	Intolerant	Avoider	Endemic	Expansion	Decline
Calocedrus decurrens	Intermediate[a]	Tolerant	Resister	Widespread	Decline	Expansion
Picea breweriana	Tolerant	Tolerant	Avoider	Endemic	Decline	Expansion
Picea engelmannii	Tolerant	Intolerant	Avoider	Southern limit	Decline	Expansion
Pinus contorta	Intolerant	Tolerant	Embracer	Widespread	Decline	Expansion
Pinus lambertiana	Intermediate[a]	Tolerant	Resister/ Invader	Widespread	Decline	Expansion
Pinus monticola	Intolerant	Intolerant	Invader	Widespread	Decline	Expansion
Pinus ponderosa	Intolerant	Tolerant	Resister	Widespread	Decline	Expansion
Pseudotsuga menziesii	Intermediate[a]	Tolerant	Invader	Widespread	Expansion	Decline
Tsuga mertensiana	Tolerant	Intolerant	Avoider	Disjunct	Expansion	Decline

Note: Species included here were found in at least 20 plots in either year. The climate change prediction shown refers to the expectation for change in overall abundance; whereas we predicted overall decline for drought-intolerant taxa, we also expected movement to higher elevations for all species. Much of the information about individual species can be found in Burns and Honkala (1990) and https://www.feis-crs.org/feis/.

[a] *Calocedrus decurrens*, *Pinus lambertiana*, and *Pseudotsuga menziesii* are intermediate in their tolerance of shade compared with the other taxa in our study area. For the purpose of our three main predictions, and based on our understanding of their autecology, we included *C. decurrens* and *Pinus lambertiana* with the shade-intolerant species and *P. menziesii* with the shade-tolerant species.

conducted in the Russian Wilderness, a 5000 ha landscape within the east-central Klamath Mountains (Figure 1). The wilderness is composed of metamorphic and granitic rock that supports primarily mixed-conifer forests and ranges in elevation from 760 to 2498 m. At lower elevations, modern forests of the area are primarily comprised of *Pinus ponderosa* (ponderosa pine), *Pseudotsuga menziesii* (Douglas-fir), and *A. concolor* (white fir); upper-montane forests contain *A. magnifica* var. *shastensis* (Shasta red fir), *Pinus contorta* (lodgepole pine), and *Pinus monticola* (western white pine); and subalpine forests contain *A. magnifica* var. *shastensis*, *Tsuga mertensiana* (mountain hemlock) and *Pinus albicaulis* (whitebark pine). In addition to the region's rich conifer diversity, the wilderness is home to more than 400 understory plant species, making it a hotspot of botanical diversity (Desiervo et al., 2016). The climate is Mediterranean with warm, dry summers and most moisture occurs as snow during cool winters.

The study area was designated as wilderness with the passing of the California Wilderness Act of 1984. Prior to this designation, timber harvesting occurred at only the lowest elevations and the vast majority of the wilderness is unlogged and harbors extensive areas of old-growth forests (Isbell, 2019). As a result, much of the wilderness is also designated as protected Forest Service Management Areas, including the Sugar Creek Research Natural Area (RNA) and the Duck Lake Botanical Area (Isbell, 2019).

Fire history in Klamath montane forests

Modern vegetation assemblages in the Klamath Mountains were established ~2000 years before present with shifts in forest composition corresponding to fluctuations in climate, fire activity, and human populations (Briles et al., 2005; Mohr et al., 2000). Drought-tolerant, fire resistant *Pinus* spp. expanded during warm, dry periods of high fire activity, whereas shade-tolerant *Abies* spp. expanded during cool periods (Briles et al., 2005; Crawford et al., 2015; Mohr et al., 2000). Native American burning near settlements at lower elevations and along travel routes in higher elevations increased fire activity during cool periods, but may have had less effect at more remote, high-elevation sites (Crawford et al., 2015). Fire activity has been relatively high over the last 2000 years and peaked in the late 19th and early 20th centuries (Briles et al., 2011), but declined during the late 20th century following the declines in Native American populations and the onset of fire exclusion (Whitlock et al., 2004).

Prior to fire exclusion, fire return intervals in lower elevation montane forests of the Klamath Mountains averaged ~15 years and ranged from ~5 to 75 years (Taylor & Skinner, 1998; Taylor & Skinner, 2003). Both the mean and range of fire frequency increased with elevation in upper-montane and subalpine forests, with a mean of 43 years and fire-free periods ranged 6 to 126 years (Coppoletta et al., 2021). During the 20th and 21st centuries, active fire exclusion led to predictable increases in fuel accumulation and shade-tolerant tree species (Dimario et al., 2018; Skinner et al., 2006; Taylor & Skinner, 1998, 2003). Within the Russian Wilderness, it is likely that at least two to four fire cycles were missed over the past century at lower and mid-elevations, although higher elevations have probably missed fewer fires (Isbell, 2019). Until 2014, no fires had occurred in the Russian Wilderness for more than a century (Safford et al., 2011). The Whites Fire of 2014 burned 1180 ha of the wilderness, and we excluded plots ($n = 7$) that burned in the fire from our study.

Assessing recent climate change in the Russian Wilderness

To quantify changes in climate between the historical and recent survey of legacy plots in the Russian Wilderness and to assess how these shifts might explain changes in forest composition and structure, we evaluated overall temporal trends in temperature and precipitation in the study area, and we explored how the magnitude of climate change varied within the complex topography of the study region. First, we assessed overall trends in climate from the 1960s to the 2000s using data derived from the parameter-elevation regression on independent slopes model (PRISM) model, which interpolates climate data from a combination of instrumental records and topographic variables (e.g., Daly et al., 2002). The climate variables we assessed were average growing season temperature, minimum temperature, maximum growing season temperature, and precipitation, and we used linear models to detect statistical changes over this 45-year period. Next, to address how climate change varied within the study area due to complex topography, we derived climate data for each plot and compared changes from 1960 to 1969 and from 2005 to 2014 using the California Basin Characterization Model (BCM), a spatially explicit hydrologic response model that downscales PRISM data to a 270-m grid resolution (Flint & Flint, 2012). The climate variables we assessed at the plot level were minimum temperature, maximum growing season temperature, precipitation, and climate water deficit (CWD). Because the BCM climate data depend on elevation and topography as part of the downscaling process, it was not statistically appropriate to relate modeled changes in climate across elevation and moisture gradients. Alternatively, we used these data to explore how the magnitude of climate changes varied with elevation and topography of the study landscape, and to inform when we might expect the greatest vegetation response (i.e., lower or higher elevations, or wetter or drier locations).

We used the overall observed temperature change across the landscape to derive expectations of movement up the elevation gradient based on the adiabatic lapse rate following similar studies (e.g., Savage & Vellend, 2015). Because adiabatic lapse rates vary between regions and are strongly influenced by humidity, we showed a range of expected changes in elevation. We showed expectations based on (1) the average of empirical measures in the western USA (0.45°C per 100 m) and (2) the measure in drier areas that might better represent our study area (0.65°C per 100 m) (please refer to Dunbar-Irwin & Safford, 2016; Tercek et al., 2021).

Historical and recent data collection

In summer 1969, Sawyer and Thornburgh (1974) collected data from 207 plots ranging from a 1300 m elevation forest dominated by *P. ponderosa* to 2469 m elevation forests dominated by *P. albicaulis* and *T. mertensiana* (Appendix S1: Figure S1). Approximately 90% of the original 207 plots fall within the area now designated as the Russian Wilderness. Sawyer and Thornburgh (1974) used a relevé protocol for sampling vegetation (Sawyer & Keeler-Wolf, 1995). Relevé plots are intended for stands with similar compositional and structural homogeneity. For all plots, Sawyer and Thornburgh (1974) recorded detailed information about each location including topographic position, slope, and aspect (Appendix S1: Figure S2). They also recorded species cover of trees in three strata: seedlings, saplings and canopy trees throughout the entire relevé area. Cover was recorded according to the following seven-rank scale: (1) one specimen; (2) sparse; (3) <10%; (4) 10%–25%; (5) 25%–50%; (6) 50%–75%; (7) more than 75%. The designation of "one specimen" was only used if that one individual occupied less ≤1% cover and was most commonly used for seedlings that were only found once in a given plot. Sawyer and Thornburgh restricted their sampling to relatively homogenous, mature vegetation stands, intentionally avoiding ecotones and areas with recent disturbance (Sawyer & Thornburgh, 1974).

In summer 2015, we attempted to relocate all of Sawyer and Thornburgh's plots within the boundary of the Russian Wilderness (156 plots). We determined plot locations first by digitizing a USGS quad map on which

Sawyer and Thornburgh (1974) had marked locations by hand (Figure 1), and georeferencing locations using ArcMap 10.1 software (ESRI, Redlands, CA). After navigating to the location, we then looked for an area that matched the aspect, slope, topographic position, and sometimes detailed descriptions by Sawyer and Thornburgh (1974) (please refer to Appendix S1: Figure S2). We limited our search radius to ~150 m from the center of the original hand-drawn plot to account for a small, but reasonable, degree of error in the demarcation of plot locations on the hand-drawn map (Figure 1). Once we had found a matching topographic location, we searched for a smaller area that matched the overstory species assemblage in 1969, with a few caveats for change over the past 46 years. For example, an overstory tree species could be missing if we found dead individuals in the area, and species could be added as canopy trees if they were present as saplings in 1969. Similarly, we looked for a close match with the understory species (which were recorded in 1969, but not used in this study); however, we acknowledge that, in some instances, particularly in lower elevation forests with high fuel accumulation, the understory could be quite different based on recent studies in other parts of the Klamath Mountains (Damschen et al., 2010; Harrison et al., 2010). Using these criteria, there were 11 instances when we searched but could not successfully relocate and resample one of Sawyer and Thornburgh's plots. In a recent study from central Europe evaluating the accuracy of legacy plot resampling techniques, Kopecký and Macek (2015) found that temporal changes inferred from vegetation resurveys were robust to a reasonable amount of uncertainty in original plot location. Our intent was not to examine changes in the abundance of species in individual plots between samplings, but rather to compare how the distribution and abundance of species had changed in our study landscape over time.

In revisiting the plots, we replicated the 1969 Sawyer–Thornburgh protocol, and conducted our fieldwork during the same months (June, July, and August). Sawyer and Thornburgh (1974) did not explicitly state the size and/or shape of their plots, however they compiled the percentage cover data to conduct ordinations and gradient analyses, therefore we felt reasonably confident in assuming they used the same plot size throughout this region. To determine the appropriate plot size for resampling, we experimented with several sizes and shapes on a reconnaissance trip to the study area using general guidelines from Sawyer and Keeler-Wolf (1995) about relevé plots in forest and woodland communities. We settled on a 16 m radius circular plot (804.25 m^2) and used this size and shape for plots. Although we cannot be certain that this was the exact plot size used by Sawyer and Thornburgh in 1969, we felt confident that the coarse estimates of cover would be robust to slight differences in plot size, especially because the plots were located within larger, compositionally homogenous stands. Similar to the original sampling, we avoided sampling in areas that were clearly ecotones or when composition changed over short distances.

We recorded the same environmental data as Sawyer and Thornburgh (see *Historical and recent data collection*), and we recorded species cover estimates of trees in the three strata (seedlings, saplings, canopy) using the seven-rank cover class scale (see Historical and recent data collection). Sawyer and Thornburgh (1974) did not explicitly state cutoff values for distinguishing seedlings, saplings, and canopy trees, therefore we used the designation used by the United States Forest Service in which seedlings represent trees <1.37 m in height, saplings were >1.37 m tall, but smaller than 7.6 cm diameter at breast height (dbh), and canopy trees were >7.6 cm dbh. Because we used the seven-rank cover scale, our ability to detect changes in distributions of different life stages over this 46-year period should be robust and conservative, regardless of uncertainty of the precise definitions of the three size classes.

To test how species distributions changed over ecological gradients, we derived elevation and a heat load index (HLI; McCune, 2007) from a 30 m digital elevation model. The HLI is a proxy for solar radiation based on aspect, slope, and topographic position in the context of surrounding landscape. To do this, we obtained Universal Transverse Mercator (UTM) coordinates using a Trimble® Juno 3B data collector (Sunnyvale, CA, USA) in 2015, rather than the coordinates georeferenced from the quad map (please refer to the preceding paragraphs), as we considered the 2015 points to be a more consistent measure of topography and more accurate than the estimates from field observers.

Species abundance and distribution analysis

Of the 156 plots we resampled, we excluded the data from seven plots due to fire, one due to missing information on the datasheet, and two due to logging disturbance. Evidence of logging in these latter two sites (i.e., stumps) was found near the road system at low elevations and presumably occurred after the 1969 sampling, but before the area was designated wilderness. Using the remaining 146 plots, we further restricted our data analysis to tree species that were found in at least 20 plots in both 1969 and 2015 to increase the power of our subsequent tests. The remaining list of species used in our analyses included 12 species, all of which were conifers (Table 1). We converted cover class values for these 12 species to median values for both years as the following: cover class (1) 1%; (2) 3%; (3) 7%; (4) 17.5%; (5) 37.5%; (6) 62.5%; and (7) 87.5%. Because higher classes included a greater range of cover, this approach was likely to underestimate the amount of change. For example, a change of 10% in a low cover class (i.e., cover classes 1, 2, or 3) would be recorded as a change from one class to another, but a 10% change would not necessarily be recorded as a change in the broader, high cover classes (i.e., cover classes 4, 5, 6, or 7).

To assess changes in cover between 1969 and 2015, we used Wilcoxon signed rank tests for all life stages (canopy, saplings, seedlings) of each species as the distributions of median values (please refer to the preceding paragraphs) were not normal. To assess change in the total cover for a species, we summed the median values of the three life stages and used Wilcoxon signed rank tests. For these tests, comparisons use any plot that had that species and life stage in either year, rather than across all plots in the study area. Because detecting changes in cover is more difficult when using data derived from broad cover classes rather than more precise estimates of percent cover, we present p-values unadjusted for multiple comparisons.

To assess whether the distribution of species along the elevation gradient changed between 1969 and 2015, we used two complimentary methods. First, we compared the distributions of species occurrence based on the presence and percentage cover of each species between 1969 and 2015. To do this, we compared the abundance-weighted mean elevations between these two years. However, because abundance-weighted mean elevations involve multiplication operations using ordinal data, we first transformed our cover data to quasimetric values. To do this, we used the "ordinal transfer value" (OTV) suggested by van der Maarel (van der Maarel, 2007) defined as $\text{OTV} = a \times \ln C + 2$, where a is a weighting factor (1.415) and C is the median cover value of the cover class (please refer to the preceding paragraphs). Transformed cover data were approximately normally distributed, and so we used t-tests to compare cover between years. These t-tests were conducted for each life stage separately, as well as on the combined total of all life stages. For the total abundance-weighted mean elevations, we summed the median values (please refer to the preceding paragraphs) of the three life stages before performing the OTV transformation. We presented the change in abundance-weighted elevations as a percentage of expected change based on perfect tracking of climate warming, in which the ~1.5°C increase in mean temperature between 1969 and 2015 (Figure 2) would result in a minimum expected increase in elevation of 230 m (Table 2).

Second, we used non-parametric multiplicative regression (NPMR) to develop species distribution models for each of the 12 conifer species. NPMR is well suited for modeling ecological relationships that are non-linear (McCune, 2006) as it makes no assumptions of the relationships between response and predictors and allows for interactions among predictors. In a comparison with similar methods, NPMR was more effective at capturing the true response shape of species distributions across environmental gradients (Lintz et al., 2011). We developed NPMR regressions for seedling, sapling, and canopy cover measures separately for each of our 12 conifer taxa using elevation, HLI, and sampling year as predictors. We used Hyperniche v.2.3 (McCune & Mefford, 2009) with a Gaussian local mean smoother and the medium over-fitting controls. Elevation and HLI were treated as continuous variables, whereas year was treated as a categorical variable. For each species/life stage combination, candidate models were evaluated using a conservative measure of model fit, xR^2, the cross-validated R^2 estimated by excluding each data point from the estimate, and the significance level of candidate models was derived from a permutation test (100 randomizations). For parameters in our models, we present the sensitivity statistic, a measure of the change in the response to a 5% shift in the predictor. For the subset of models in which year was included as a predictor in the best-fit model, we further evaluated if there was a year × elevation or HLI × elevation interaction by generating point-wise confidence intervals of the model estimates ("variability bands"). This allowed us to assess visually how the distribution of cover along the elevation and HLI gradients changed between the two survey dates.

Community composition and beta-diversity analysis

We used non-metric multidimensional scaling (NMS) to examine changes in community composition of trees over the sampling period with the *vegan* package (Oksanen, 2009) in R (R Core Team 2019). NMS is an indirect ordination technique that ranks plots in order of compositional similarity and reduces the dimensionality to a few primary axes representing the major gradients in species composition. We used the same median-converted cover classes that is appropriate for NMS (Podani, 2006). We square root transformed each species cover and used the Bray–Curtis index based relativized by total plot cover. We began with five axes ($k = 5$), then reduced the dimensionality until an optimal solution with minimal stress using the fewest number of axes was found. We then assessed the relationship between each of the axes with elevation and HLI using the "envfit" function to perform a non-parametric test with 999 permutations.

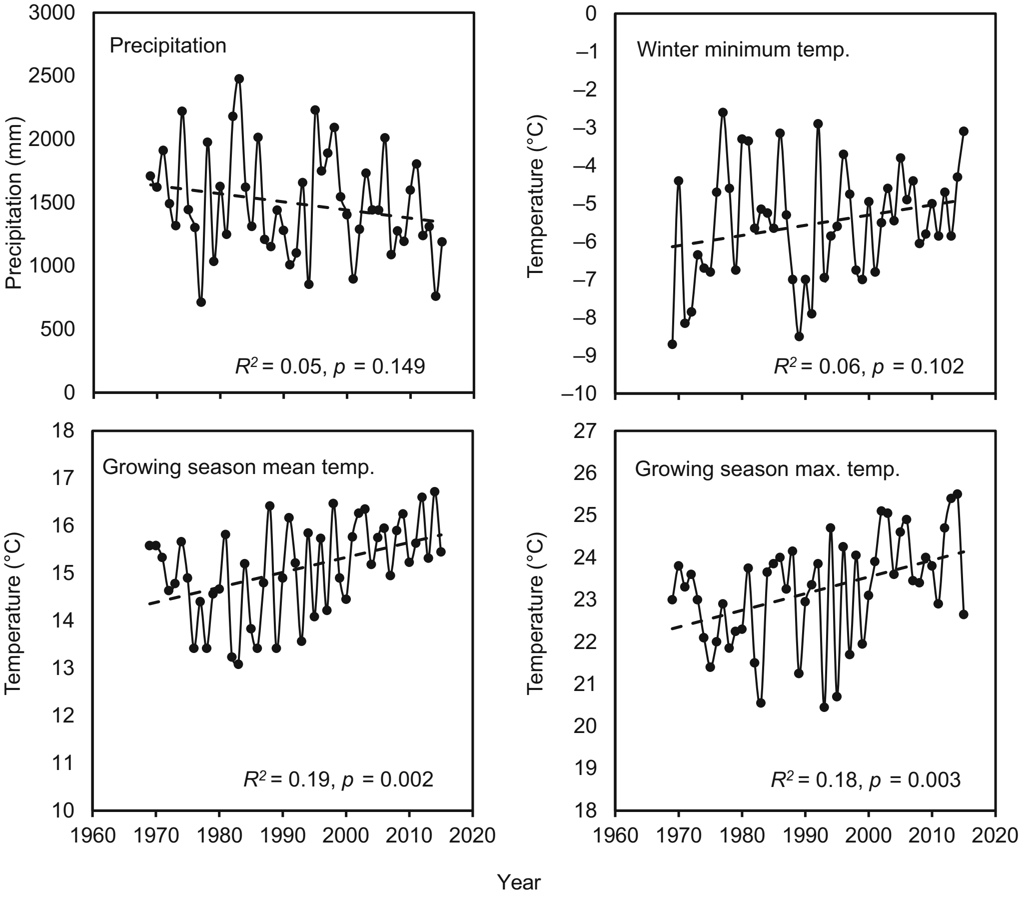

FIGURE 2 Climate data for the study watershed in the Klamath Mountains of California, USA, from 1969 to 2015. Data are derived from the parameter-elevation regression on independent slopes model (PRISM) model, which interpolates climate data from a combination of instrumental records and topographic variables (Daly et al., 2002). We used an average of two 2-km grid cells that covered the majority of the watershed. Precipitation is annual water year (October–September), winter temperature includes December–February, and growing season temperature includes June–August. Simple linear regressions are shown for each of the four climate variables used.

We used two approaches to test for shifts in species composition. First, we used a multiple response permutation procedure (MRPP; McCune et al., 2002) to test the hypothesis of no difference in homogeneity of species composition. The MRPP also provides a description of the effect size (A) that ranges from 0 to 1 ($A = 1$ when composition is identical) based on the weighted mean within-group distance (delta). Second, we tested for shifts in composition along the elevation and HLI gradients following Damschen et al. (2010). We rotated the ordination to maximize correlation with each of the two environmental gradients and Axis 1, and then used a Wilcoxon signed rank test to test the hypothesis of no difference in mean ordination scores between 1969 and 2015.

We explicitly compared changes in beta-diversity along gradients in elevation and HLI using Mantel tests and the decay in similarity as a measure of the rate of species turnover along environmental gradients (Nekola & White, 1999). This metric of beta-diversity is influenced by the abundance of each species across a landscape, as well as the degree of species aggregation along environmental gradients (Morlon et al., 2008). Mantel tests use Monte Carlo randomizations to test the strength of correlative relationships between two matrices, in this case between the decay in compositional similarity and environmental distance. The slope of the regression provides an estimate of the rate of species turnover and the correlation coefficient is a measure of the strength of the gradient in structuring species turnover. We then fitted exponential distance decay functions for elevation and HLI for each year using the R package *betapart* and performed a permutation test following (Nekola & White, 1999) to test for differences in slopes between the two years using the "diffslope" function in the R package *simba*.

TABLE 2 Mean elevations for 12 conifers observed in 1969 and 2015 in the Klamath Mountains of California, USA.

Species	1969 mean elevation (m)	2015 mean elevation (m)	Elevation change (m)	Elevation change per decade (m)	Percent of expected change based on warming[a]	t	p
Abies concolor	1792	1838	46.0	10.0	14%–20%	−1.77	0.077
Abies lasiocarpa	2061	2067	5.9	1.3	2%–3%	−0.39	0.700
Abies magnifica var. *shastensis*	2047	2052	5.1	1.1	2%	−0.24	0.810
Calocedrus decurrens	1599	1669	70.2	15.2	21%–31%	−2.72	**0.007***
Picea breweriana	1926	1902	−24.5	−5.3	−7% to −11%	1.08	0.280
Picea engelmannii	1829	1855	24.8	5.4	7%–11%	−1.49	0.137
Pinus contorta	1995	1990	−4.6	−1.0	−1% to −2%	0.26	0.793
Pinus lambertiana	1630	1648	18.4	4.0	6%–8%	−1.08	0.280
Pinus monticola	2034	2046	12.0	2.6	4%–5%	−0.69	0.491
Pinus ponderosa	1659	1612	−47.2	−10.3	−14% to-21%	2.25	**0.025***
Pseudotsuga menziesii	1703	1727	24.0	5.2	7%–10%	−1.02	0.306
Tsuga mertensiana	2076	2082	6.0	1.3	2%–3%	−0.28	0.777

Note: Mean elevation is weighted by the OTV transformation of the sum of total cover of each species (i.e., all life stages combined; please refer to the text for details). The change in the means is compared with a t-test, and we present results using unadjusted p-values. Similar comparisons for separate life stages are shown in Appendix S1: Table S2.

[a] Because adiabatic lapse rates vary between regions and are strongly influenced by humidity, we show a range of expected changes in elevation. We show expectations based on (1) the average of empirical measures in the western USA (0.45°C per 100 m) and (2) the measure in drier areas that might better represent our study area (0.65°C per 100 m). Using these lapse rates and a 1.5°C increase in mean temperature of the study period (Figure 2), we estimated an expected 230–333 m increase in elevation if species were tracking changes in temperature over 46 years, or 50.3–72.5 m per decade (please refer to Dunbar-Irwin & Safford, 2016; Tercek et al., 2021).

*$p \leq 0.05$.

RESULTS

Recent climate change in the Russian Wilderness

Across the 46-year period of our study (1969–2015), we found a 1.5°C increase in mean growing season temperature, a 1.2°C increase in winter minimum temperature, and a 18% decline in annual precipitation (Figure 2). Using the average lapse rate for the western USA and the lapse rate for drier areas (please refer to *Methods*), and a 1.5°C increase in mean temperature of the study period (Figure 2), we estimated an expected 230–333 m increase in elevation if species were tracking changes in temperature over 46 years, or 50.3–72.5 m per decade (please refer to Dunbar-Irwin & Safford, 2016; Tercek et al., 2021).

Within the study area, changes in temperature were more pronounced across the elevation gradient than changes in precipitation or CWD (Appendix S1: Figure S3). In fact, the BCM estimated that CWD was greater in the 1960s compared with the 2000s (Appendix S1: Figure S3). The increase in minimum temperature was greater at lower elevations (~2.25°C at 1200 m) than higher elevations (~1.25°C at 2400 m), however; the change in maximum growing season temperature was greater at higher elevations (~1.5°C at 2400 m) than lower elevations, where there was almost no change between historical and recent periods (Appendix S1: Figure S3). HLI was not an important predictor of the magnitude of climate change within the study area (Appendix S1: Figure S3).

Species abundance and distribution

In the 146 resampled plots in our study, we found 19 tree species, including 14 conifers, 12 of which were found in at least 20 plots in both 1969 and 2015 (Table 1; all data available at DeSiervo & Jules, 2022). The most abundant species were *Abies magnifica* var. *shastensis*, *T. mertensiana*, *A. concolor*, and *P. monticola*, (Figures 3 and 4). Of these, both *Abies* and *T. mertensiana* were found across the widest range of both elevation and HLI gradients in both years (Figure 5; Appendix S1: Figure S4). *Pinus monticola*, although dispersed widely across our plots, had lower average cover than the other dominant taxa (Figure 4). Species found in fewer than 20 plots included three conifers (*P. albicaulis*, *Pinus jeffreyi* [Jeffrey pine], and *Taxus brevifolia* [Pacific yew]) and four angiosperms (*Acer macrophylla* [bigleaf maple], *Quercus chrysolepis* [canyon live oak], *Quercus kelloggii* [California black oak], and *Quercus garryana* [Oregon white oak]).

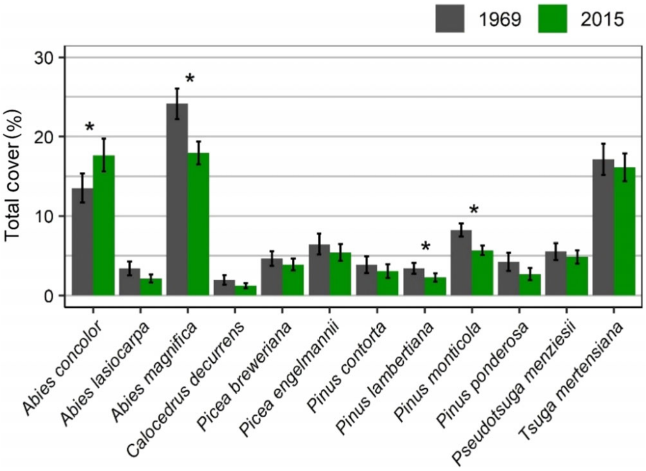

FIGURE 3 Total percentage cover of 12 conifer species measured at two survey dates, 1969 and 2015, in the Klamath Mountains of California, USA. Total percentage cover is the mean total percentage cover (seedlings, saplings, and canopy measures summed) among any plot that had that species in either year, rather than across all plots in the study area. Cover values at the plot level were recorded using a seven-rank scale and later converted to median values, which we used here to calculate total cover (see *Species abundance and distribution analysis*). Error bars indicate ±1.0 standard error (SE). Cover was compared between years using a Wilcoxon signed rank test. We present results using unadjusted p-values in which '*' indicates $p \leq 0.05$.

The biggest change in cover we observed between 1969 and 2015 was for *A. concolor*, a shade-tolerant, fire-intolerant species, which increased from 13.5% to 17.6% (i.e., 30.7% increase; Figure 3). The canopy layer of *A. concolor* increased by 24% (Figure 4) and the frequency of plots that had *A. concolor* in the canopy also increased markedly (from 48 [32.4%] to 71 [48%] plots). The number of plots with any *A. concolor*, including saplings and seedlings, increased from 64 [43.2%] to 84 [56.7%] plots.

In addition to *A. concolor*, all other 11 species experienced cumulative declines between 1969 and 2015 (Figures 3 and 4). Significant decreases were found in total cover for six of the 11 species (Figure 3). Notably, *A. magnifica* var. *shastensis* declined by 25.8%, *P. lambertiana* by 33.1%, and *P. monticola* by 30.8% (Figure 3). The canopy decreased for two shade-intolerant species; *P. lambertiana* decreased by 27.3% and *P. ponderosa* by 29.6% (Figure 4; Appendix S1: Table S1). In addition, significant decreases were found in saplings of four shade-tolerant species (*A. lasiocarpa*, *A. magnifica* var. *shastensis*, *P. menziesii*, and *T. mertensiana*) and three shade-intolerant pines (*P. contorta*, *P. lambertiana*, and *P. monticola*), and significant decreases were found for seedlings of *A. magnifica* var. *shastensis* and *P. engelmannii* (Engelmann spruce; Figure 4).

Nine of 12 species moved upward between 1969 and 2015 an average of 23.6 m (or 5.1 m per decade), and this represents only 7%–10% of the expected movement if a species was perfectly tracking climate warming. The elevation increase was significant for total cover of *C. decurrens* but not for any individual life stage of any species (Table 2; Appendix S1: Table S2). Considering all 12 species, the average upward movement was 11.3 m (2.6 m per decade; Table 2). The greatest upward movements were observed for *Calocedrus decurrens* (incense cedar; 70.2 m total), *A. concolor* (46.0 m), and *P. engelmanii* (24.8 m). We also observed a significant decrease in elevation of *P. ponderosa* (−47.2 m; Table 2) due to the loss of cover at higher elevations (Figure 5).

In addition to these changes in mean elevation, there were some more subtle, but notable, changes in the elevational distribution from 1969 to 2015 (Figure 5). For instance, we found a slight increase in the median and upper quartile abundance for the canopy of *A. concolor*, *A. lasiocarpa*, *C. decurrens*, *P. engelmannii*, and *P. lambertiana* (Figure 5). In addition, the upper and lower elevational range limits of some species changed based on changes in one or a few plots. For instance, *A. concolor* and *P. lambertiana* were each found in the canopy of plots 226 and 136 m higher, respectively, where there had been no seedlings or saplings in 1969. Seedlings were established at higher elevations in 2015 for four taxa: *A. concolor*, *C. decurrens*, *P. engelmannii*, and *P. menziesii* (Figure 5). The lower elevation limit of *P. engelmannii*, *P. monticola*, and *P. ponderosa* canopy trees all increased because a single plot occupied in 1969 no longer had these species in 2015 (an increase in 75, 44, and 24 m, respectively). The lower elevation limit of *A. magnifica* var. *shastensis* canopy trees increased by 73 m as two plots occupied in 1969 no longer had canopy trees in 2015. It is important to note that we did not base any of our conclusions about elevational shifts on changes that occurred in just a few plots. Alternatively, we relied on our comparison of abundance-weighted mean elevations (please refer to the preceding paragraphs).

Using NPMR, we produced a single best-fit model for cover of each life stage of each species, for a total of 36 models (12 species × 3 life stages; Appendix S1: Table S3). Of these, only six included year as a predictor of cover (Table 3). When we evaluated these six models using the bootstrapping method to produce variability bands, only four models showed clear year × elevation interactions (models for *A. concolor* canopy, *A. magnifica* var. *shastensis* saplings and seedlings, and *P. monticola* saplings). Of those, the models for *A. magnifica* var. *shastensis* saplings and seedlings, and *P. monticola* saplings indicated declines between 1969 and 2015 in the middle portion of the elevation range. In contrast, an increase in the canopy life stage at mid-elevations was evident for *A. concolor* (Figure 6). We found no year × HLI interactions in any of our models. In most models, estimates of cover were considerably more sensitive to elevation than

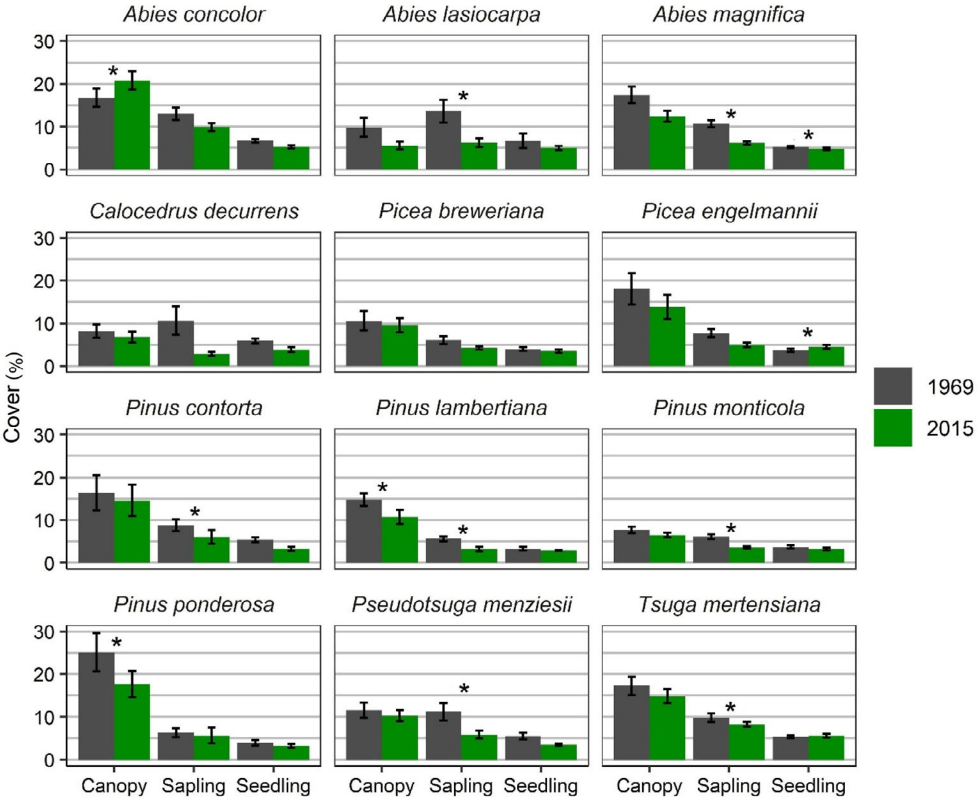

FIGURE 4 Percentage cover of canopy trees, saplings, and seedlings of 12 conifer species measured at two survey dates, 1969 and 2015, in the Klamath Mountains of California, USA. Percentage cover is the percentage cover among any plot that had that species and life stage in either year, rather than across all plots in the study area. Cover values at the plot level were recorded using a seven-rank scale and later converted to median values, which we used here to calculate total cover (see *Species abundance and distribution analysis*). Error bars indicate ±1.0 standard error (SE). Cover was compared between years using a Wilcoxon signed rank test. We present results using unadjusted *p*-values in which "*" indicates $p \leq 0.05$.

HLI, and this was true in all models that included all three explanatory variables (Table 3; Appendix S1: Table S3).

Community composition and beta-diversity

The final NMS ordination resulted in a two-dimensional solution with a final stress of 0.169. Axis 1 had a strong, significant correlation with elevation ($r^2 = 0.74$, $p < 0.001$), and Axis 2 had a weak correlation to HLI ($r^2 = 0.08$, $p < 0.001$; Figure 7). The results of the MRPP tests found no change in homogeneity of tree species composition between 1969 and 2015 ($p = 0.346$, $A = 0.0002$, $\text{delta}_{1969} = 0.588$, $\text{delta}_{2015} = 0.573$). However, paired *t*-tests of plot scores rotated to maximize correlation with elevation were slightly but significantly lower ($W = 7260$, $p < 0.0001$) in 2015, indicating a slight shift toward lower elevation species composition. There was no significant change along the HLI gradient ($t = 0.298$, $p = 0.760$).

Mantel tests found a significant negative relationship between community similarity and pairwise differences in elevation in both 1969 ($r = -0.608$, $p = 0.001$) and 2015 ($r = -0.614$, $p = 0.001$), indicating a strong relationship between species turnover and elevation for both years (Figure 8). We detected a significant ($p = 0.001$), but small, decrease in the slope of the distance decay function between 1969 and 2015 (Table 4), indicating that beta-diversity and the rate of change in compositional turnover across the elevation gradient was slightly lower in 2015 compared with 1969. Mantel tests found a weak, but significant, negative relationship between compositional similarity and HLI for 2015 ($r = -0.056$, $p = 0.029$), but no significant relationship in 1969. Similarly, the distance decay functions detected significant but weak relationships for HLI in 2015 (pseudo-$r^2 = 0.01$, $p = 0.001$,) but not 1969 (Table 4). There was a significant ($p = 0.004$) increase in the slope of the distance decay function for HLI between 1969 and 2015, indicating a slight increase in beta-diversity and species turnover along the gradient in HLI (Figure 8).

DISCUSSION

Over a half a century, we documented a large increase in cover for one tree species, significant declines in total cover for six species, and declines in early life stages for

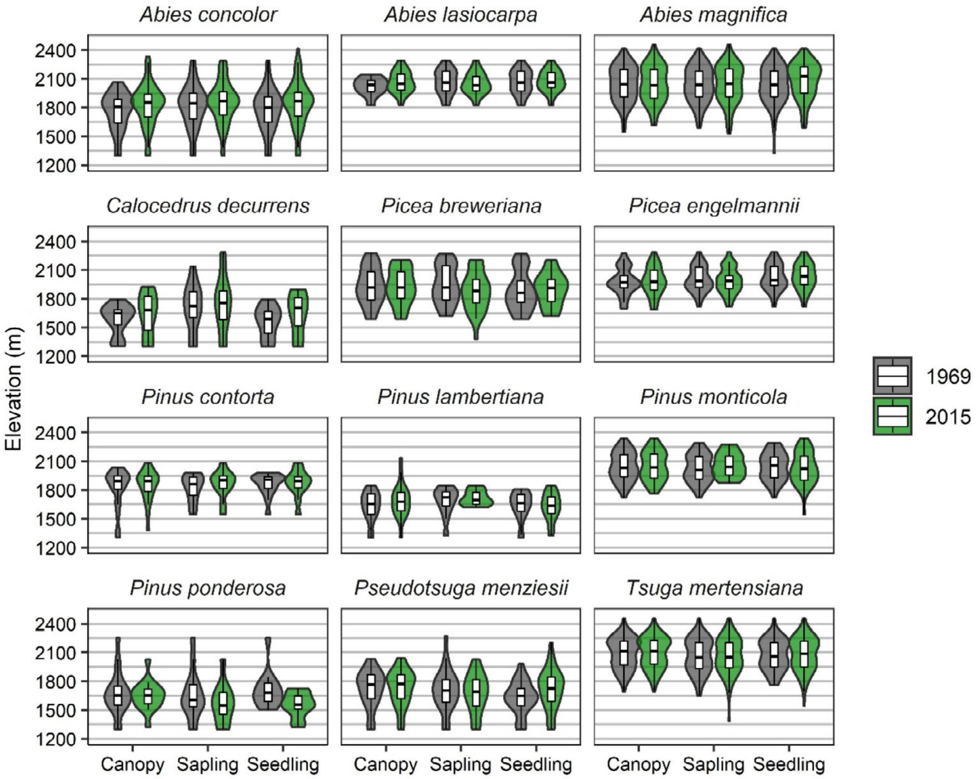

FIGURE 5 Violin plots showing the distribution of 12 conifer species across an elevation gradient, where plots were first sampled in 1969 (gray) and then resampled in 2015 (green) in the Klamath Mountains of California, USA. The violin shapes show the density of occupied plots at each elevation and the box plots show quartiles of occupied plots along each gradient. Please refer to Table 2 and Appendix S1: Table S2 for abundance-weighted mean elevations used in statistical analyses (please refer to *Methods* for details).

TABLE 3 Summary of non-parametric multiplicative regression (NPMR) models used to evaluate changes in the relationship with elevation and moisture between 1969 and 2015 for different life stages of 12 conifer species.

Species	Life stage	Predictors	xR^2	n	Elevation sensitivity	HLI sensitivity
Abies concolor	Canopy	Year, elevation	0.400	119	0.496	…
Abies magnifica var. *shastensis*	Sapling	Year, elevation, HLI	0.125	219	0.228	0.011
	Seedling	Year, elevation, HLI	0.122	200	0.284	0.069
Calocedrus decurrens	Sapling	Year, elevation, HLI	0.321	23	0.064	0.042
Pinus monticola	Sapling	Year, elevation	0.193	113	0.517	…
Pseudotsuga menziesii	Sapling	Year, elevation, HLI	0.495	53	0.189	0.100

Note: Models that explained the most variation in cover were selected based on xR^2, the cross-validated R^2. Models shown are those in which year was a predictor in the selected model; the set of full models for all species/life stages combinations are shown in Appendix S1: Table S3. HLI indicates heat load index (please refer to the text for details). The significance for all models shown is $p < 0.01$, in which p is the proportion of randomization runs from a Monte Carlo simulation that resulted from the original model (McCune, 2006). Sensitivity values indicate the change in the response variable (species cover) to a 5% shift in the predictor variable.

the remaining five species. Although directional changes in abundance were often consistent among taxa with similar life history traits, species responded individualistically (Whitlock et al., 2004) to recent warming and varied even within genera (e.g., *Abies*). Drought-tolerant, early-seral species showed significant declines due to the loss of canopy trees, whereas declines in early life stages (i.e., seedlings and saplings) in late seral species at high elevations suggest that multiple species may show lagged responses and are on the verge of greater declines. We also observed consistent, but mostly non-significant, upward shifts for nine out of 12 species that were far less than expectations based on recent warming, and a relatively high degree of inertia at the community level.

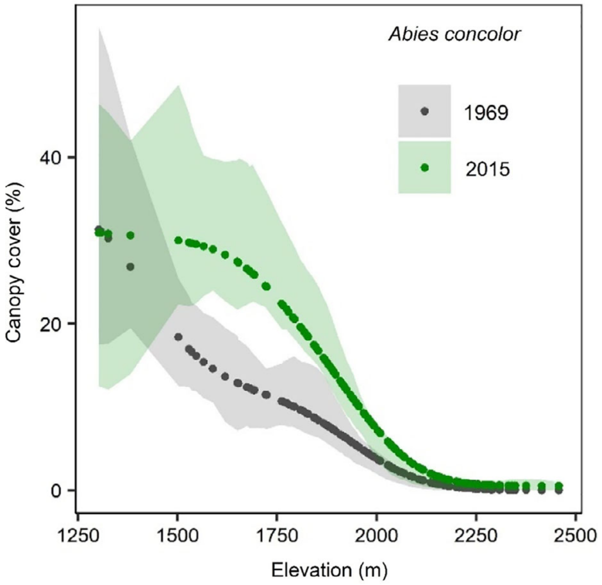

FIGURE 6 Predictions of cover from the non-parametric multiplicative regression (NPMR) model for the canopy layers of *Abies concolor* in the Klamath Mountains of California, USA. Mean model estimates are shown for 1969 (black) and 2015 (green) using larger circles, whereas smaller circles show variability bands, which are the 5th and 95th percentile point-wise confidence intervals of the model estimates.

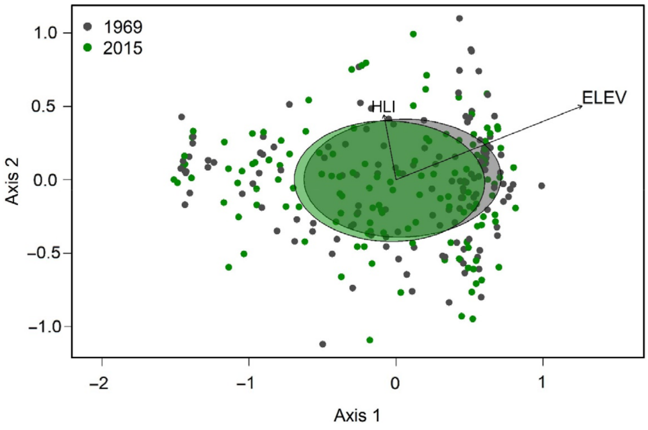

FIGURE 7 Ordination from non-metric multidimensional scaling ordination of total cover of tree species in 146 plots in the Klamath Mountains of California, USA, in 1969 and 2015. Environmental vectors are represented by arrows in which the length represents the correlation with elevation and heat load index (HLI). Ellipses represent two standard deviations of a weighted mean of all plot scores for each time.

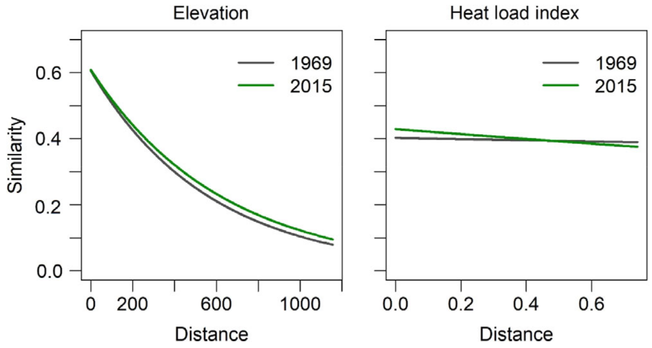

FIGURE 8 Results of distance decay functions for elevation and heat load index (HLI) for 1969 and 2015 in 146 plots in a montane landscape in the Klamath Mountains of California, USA. We used Mantel tests that regress distance matrices to test the relationship between the decay in compositional similarity and environmental distance (Table 4). The slope provides an estimate of the rate of species turnover and the correlation coefficient is a measure of the strength of the gradient in structuring species turnover.

Our study is emblematic of the challenges in predicting shifts in species distributions and emergent change in diverse communities where species exhibit variable responses to the complex suite of changing conditions. The changes we observed in cover and elevation were often not statistically significant, yet strikingly consistent among species in their direction (Table 2; Figures 3 and 4). In addition, the changes in community composition we observed using multivariate analyses were relatively minor compared with those we observed for individual species. In the following paragraphs we examine our observations for each set of predictions we made and follow with a discussion of how the potential limitations of the relevé method might suggest that our study is indicative of even larger changes.

Shade-tolerant species

In support of our first hypothesis, we found a significant increase in the abundance (30.7%) of *A. concolor*, the least drought-tolerant species, at lower and mid-elevations in our study area. The initial impacts of fire exclusion on shade-tolerant species were already apparent when Sawyer and Thornburgh collected data in these forests in 1969. They recorded these ongoing changes in the lower-montane zone on several datasheets noting “open forests being encroached by white fir and Douglas-fir” and “young forest” (i.e., presumably seedlings and saplings of *A. concolor*). In our resurveys of these plots, we found that the “young trees” documented in 1969 grew into the canopy strata over the last 46 years.

Observations on *A. concolor* are consistent with several studies across warmer, drier parts of the western USA that document increases in this species attributed to 20th century fire exclusion (Dolanc et al., 2013; Dolanc, Safford, Dobrowski, & Thorne, 2014; Minnich et al., 1995; Nelson et al., 2021; Taylor, 2000; Vankat, 2011). However, these

TABLE 4 Results of distance decay functions for elevation and heat load index (HLI) for 1969 and 2015.

Variable	Intercept	Slope	Pseudo-r^2	p
Elevation 1969	0.645	−0.0018	0.345	0.01
Elevation 2015	0.599	−0.0016	0.357	0.01
HLI 1969	0.416	−0.511	0.0001	0.23
HLI 2015	0.422	−0.217	0.003	0.01

Note: We used Mantel tests that regress distance matrices to test the relationship between the decay in compositional similarity and environmental distance. The slope provides an estimate of the rate of species turnover and the correlation coefficient is a measure of the strength of the gradient in structuring species turnover.

studies primarily document increases in saplings and small trees, whereas we observed changes in larger canopy trees, suggesting a greater and potentially more persistent effect of fire exclusion in the more productive forests of the Klamath Mountains. Changes in the abundance of *A. concolor* were greatest at middle elevations (Figure 6). We also detected a modest increase in the mean elevation of *A. concolor*, similar to Kelly and Goulden (2008) who found that *A. concolor* had moved upward 32 m per decade in Southern California (USA).

Paleoecological studies across the region indicate that *P. menziesii* and *Abies* spp. (*A. concolor* at lower elevations and a mix with *A. magnifica* var. *shastensis* at high elevations) have been increasing for more than 4000 years and peaked within the last several centuries in response to cooler and wetter conditions during the late Holocene, and despite relatively high fire activity (Briles et al., 2005; Briles et al., 2011; Crawford et al., 2015). A recent analysis of vegetation change in the Klamath Mountains used historical data from the Public Land Survey System and estimated that the biomass of *Abies* spp. (*A. concolor* and *A. grandis*) had increased five times and *P. menziesii* increased 1.8 times since the late 1800s (Knight et al., 2020). Despite consistent warming over the last century, our results indicated that *P. menziesii* and *A. concolor* have continued to expand their realized niche from fire exclusion and will probably continue expanding their fundamental niche to higher elevations under projected future warming.

Changes in *A. magnifica* var. *shastensis*, the other most common shade-tolerant species in our study area, were substantially different from its congener *A. concolor*. We observed an overall decrease of 25% for *A. magnifica* var. *shastensis* (Figure 3) that was consistent with our hypothesis based on declines in *Abies* during the warm periods in local high-elevation paleostudies (Briles et al., 2011) and an extensive recent mortality event documented in our study area and other parts of the species range (DeSiervo et al., 2018; Mortenson et al., 2015). The mortality event is caused by a disease complex of dwarf mistletoe (*Arceuthobium abietinum* subsp. *wiensii*) and a canker-forming fungus *Cytospora* that increases susceptibility to the native bark beetle, fir engraver (*Scolytus ventralis*). The disease complex tends to be most impactful in older stands (DeSiervo et al., 2018) and in warmer sites at upper elevations that have experienced more canopy decline relative to those in cooler, topographically sheltered sites (Bost et al., 2019). Fire exclusion and a cooler, wetter mid-20th century climate probably facilitated an expansion of *A. magnifica* var. *shastensis*, a relatively drought-tolerant species (Waring et al., 1975) to drier sites at higher elevations, but left this species vulnerable to spatially contagious biotic mortality agents during recent droughts. Therefore, this recent mortality event for *A. magnifica* var. *shastensis* exemplifies how two global change drivers, fire exclusion and climate warming, can interact in driving recent tree mortality.

Interestingly, our findings for *Abies* spp. contrast those from a recent study from the Sierra Nevada that found little change in *A. magnifica* var. *magnifica* and a substantial decline in *A. concolor* saplings at the ecotone boundary, over a shorter, more recent period (1981 and 2016) with substantial warming (+0.5°C) and increased CWD (Nelson et al., 2021). This highlights how species responses may be variable across different parts of their range, in which climate change has had differential impacts (i.e., increased drought and CWD in the Sierra Nevada compared with the Klamath bioregion; Rapacciuolo et al., 2014).

Species near their southern range limit and high-elevation species

Similar to other high-elevation species (Harsch et al., 2009), we found mixed support for our predictions about changes in abundance of the high-elevation conifer species at the southern end of their range. *Abies lasiocarpa* experienced significant declines in total cover, whereas other species only experienced significant declines in early life stages, and only *P. engelmannii* moved upward (7%–11% of what would be expected had they been tracking climate warming, respectively; Table 2). Conlisk et al. (2017) found a similar result in the Rocky Mountains (USA) for *P. engelmannii*, for which reductions at the lower elevation margin were greater than the expansion of the species upward. Despite upward migration observed at the treeline for many high-elevation species around the world (e.g., Harsch et al., 2009) and increased opportunities for establishment at upper elevations with earlier declines in snow cover caused by warming, upward migration at high elevations is limited by dispersal and expansion to warmer and drier upper ridges, which may be unlikely as these sites are prone to earlier and more intense late season drought.

Declines in early life stages (i.e., seedlings and saplings) suggest that high-elevation species are on the verge of greater declines that will lead to long-term changes in overall abundance (Kobe, 1996) in the absence of recruitment to offset recent and ongoing mortality and canopy decline from insects and pathogens (Bost et al., 2019; DeSiervo et al., 2018). Sapling declines for *A. lasiocarpa* are attributed to the same disease complex affecting *A. magnifica* var. *shastensis*, as well as the invasive sap-sucking insect, Balsam woolly adelgid (*Adelges piceae*) (DeSiervo et al., 2018). For *P. engelmannii*, our observation of reduced seedlings is in agreement with those of Conlisk et al. (2017); the lagged response at higher elevations they found in the Rocky Mountains was due to differences in seedling recruitment across climate gradients. Reduced seedling recruitment has also been observed in Oregon and Washington (Monleon & Lintz, 2015), as well as the Rocky Mountains (Kueppers et al., 2017), where it is linked to the reduced snowpack (Andrus et al., 2018).

The endemic *P. breweriana* and *T. mertensiana* were the high-elevation species with the lowest levels of decline, only experiencing significant or marginally significant declines in their sapling layers (Figure 4; Appendix S1: Table S1). These findings were surprising for *T. mertensiana*, a disjunct population that has been increasing and expanding downslope over the last 1500 years in response to late Holocene cooling in our study area (Briles et al., 2005), and is much more common in moister parts of its range. By contrast, *P. breweriana* is the most drought tolerant of all upper-montane tree species (Waring et al., 1975). This species is closely related to a Miocene species that was previously distributed across a much greater extent of the western USA and is more closely related to *Picea* species in northeastern Asia than the local congener, *P. engelmannii* (Chaney et al., 1944). Although our results suggested only minor declines in *P. breweriana*—some of which is seen at higher elevations (Figure 5)—a systematic evaluation of long-term dynamics across its range is needed to fully evaluate the response of this species to recent warming.

Although paleostudies demonstrated that high-elevation species persisted during warmer periods throughout the Holocene (Briles et al., 2011; Raven & Axelrod, 1978) and modeling exercises supported the existence of climate refugia in the region (Michalak et al., 2020; Thorne et al., 2020), our work is the first to our knowledge that has assessed long-term changes in high-elevation tree populations in the Klamath Mountains in response to recent warming. Slow and modest upward migration for these species, coupled with modest population declines, suggested a lagged climate response and questions the potential for upper-montane forests to serve as climate refugia unless populations can persist in situ within topographic refugia. Bost et al. (2019) further supported the importance of topographic refugia and found that remotely sensed canopy decline in the Russian Wilderness was greater on upper slopes and ridges compared with in more topographically sheltered sites. These results suggested that topographic complexity may buffer cooler, wetter sites from mortality associated with warming, but most species (e.g., *Picea* spp. and *A. lasiocarpa*) are already limited to cooler, more mesic sites (Appendix S1: Figures S4 and S5) and the minor declines we observed may be too subtle to be detected by remote sensing.

Shade-intolerant species

Our third prediction that shade-intolerant species would decline due to fire exclusion was supported. *Pinus* spp. and *C. decurrens* reached their peak abundance in the early Holocene when fire activity was high, and conditions were warmer and drier than at present. However, all *Pinus* spp. in our study experienced a significant decline in at least one life stage and the canopies of the two most drought-tolerant species, *P. lambertiana* and *P. ponderosa*, declined by 30% and 37%, respectively (Figure 4). Fire exclusion has probably resulted in increased competition for moisture with shade-tolerant species (e.g., *A. concolor*), reducing recruitment opportunities for shade-intolerant species, particularly at lower elevations. As competition increases and light and moisture becomes more limiting, trees become increasingly susceptible to insects such as bark beetles, which have been major drivers of recent mortality for some *Pinus* spp. in our study area (DeSiervo et al., 2018) and across western North America (Bentz et al., 2010; Kolb et al., 2016). Surprisingly, the invasive pathogen white pine blister rust (*Cronartium ribicola*) was relatively uncommon in our study area and did not account for any mortality in *P. monticola* and *P. lambertiana* (DeSiervo et al., 2018), which stands in contrast with other regions of the western USA (Keane et al., 2011).

We found support for significant upward elevation shifts for *C. decurrens*, although this represented only 21%–31% of what would be necessary to track warming (Table 2). We also found weak support for upward elevation shifts for *P. lambertiana* and *P. monticola*, whereas *P. ponderosa* had a significant decrease in mean elevation (−47 m). The slow movement along the elevation gradient we observed for most shade-intolerant species is consistent with a study across California, Oregon, and Washington that found no elevation increase for any of the shade-intolerant taxa that we had studied (Monleon & Lintz, 2015). *Calocedrus decurrens*, which is more shade tolerant than the other early-seral species and does not necessarily require bare mineral soil for establishment, moved upward more than any other species in our study (70 m). Interestingly, we were not able to detect a year × elevation interaction and this is most likely to be because the ability to detect change using NPMR (please refer to *Results*) would be limited given the high variability of cover at the elevation margin. *Calocedrus decurrens* occurred at sites ~800 m higher during the warmer, drier early Holocene (Briles et al., 2005), but such changes may occur on longer times scales than that of our study, and we anticipate that this species will continue to move upward.

Lack of more rapid upward migration of drought-tolerant, early-seral species is probably related to the lack of fire, a major catalyst of change in the paleorecord (Briles et al., 2005; Crawford et al., 2015). Most shade-intolerant species require high levels of light and bare mineral soil for regeneration (Agee, 1993), therefore expansion is unlikely in the absence of fire. Furthermore, increased canopy cover from the expansion of *A. concolor* has reduced canopy gaps and recruitment opportunities for shade-intolerant species. Recent fires have resulted in upward shifts of shade-intolerant species in other parts of the Pacific Northwest (Busby et al., 2020), but the decoupling of warming and fire activity resulting from increased dominance of shade-tolerant, drought-intolerant species at the expense of fire- and drought-tolerant early-seral species will leave this landscape less resilient to future high-severity fires and projected warming.

Beta-diversity and community-level change

Our results are consistent with the premise that fire exclusion homogenizes composition at landscape scales (Li & Waller, 2015), but the relatively minor directional change we observed suggested that community-level changes due to an expansion or decline in a few species were buffered when species richness is high and overall dominance is low. Even the large increase we observed in *A. concolor* (30.7%) only shifted mean cover of this species from 13.5% to 17.6%, whereas declines in *P. ponderosa* and *P. lambertiana* were only in the order of 1–1.5% cover (Figure 2). These changes resulted in a significant, but slight, weakening of the elevation gradient with a shift toward composition of lower elevation species that appears to be driven primarily by the increased abundance of *A. concolor* at low to middle elevations as well as its expansion upward (Figures 5 and 6), as opposed to the upward migration of more drought-tolerant species that are more restricted to lower-montane forests.

The secondary role of topography (HLI) is consistent with Whittaker (1960) who in his study depicted most of the overall beta-diversity and species turnover among communities as a response to elevation as opposed to the topographic moisture gradient. We found that low-elevation species were generally less sensitive to HLI than high-elevation species (Table 3; Appendix S1: Table S3), and high-elevation species had a much greater degree of separation in the ordination (Appendix S1: Figure S5). The strength of the HLI gradient was relatively weak overall and insignificant in 1969, although its strength did increase between the two time periods with compositional similarity among plots decreasing with greater differences in HLI in 2015. The increase in the strength of the HLI gradient appears primarily due to declines in *A. magnifica* var. *shastensis*. Although the sensitivity of HLI was low in the species distribution models, HLI was included in the final models for seedling and saplings of this species that both experienced significant declines.

The modest decline of most species and the expansion of just a single species resulted in only slight changes in beta-diversity and species turnover at the community level. This is to be expected, given that processes operating at lower levels of organization (i.e., species) are generally slow to manifest themselves at higher levels (i.e., communities; Allen & Hoekstra, 1992). Furthermore, the long-lived nature of conifers may further delay community-level responses compared with that of shorter lived organisms. In another legacy plot study of low-elevation forests in the Klamath Mountains of Oregon, (i.e., the Siskiyou Mountains), Damschen et al. (2010) found a similar stability of tree communities. However, they also found shifts in herbaceous understory communities between 1940 and 2007 that were consistent with expectations due to climate warming, including reduced cover of species with northern biogeographic affinity and an increase in species with southern affinities. These changes suggest that understory vegetation is a far more sensitive indicator of potential future changes in forest communities. Although not included in our analysis, Sawyer and Thornburgh (1974) did collect detailed data on understory communities and an analysis of rare or sensitive understory species or community-level change could provide additional insight into future vegetation changes in forests of the Klamath Mountains. It is important to note, however, that our measures of species cover and community-level change are influenced by the relevé sampling method, which uses coarse cover estimates and often focuses on homogenous vegetation. How these qualities influence analyses using legacy studies are important considerations.

Considerations of legacy studies and the relevé approach

Despite the obvious value of legacy plot studies in documenting long-term change, they have inherent limitations and considerations, and these have been discussed by numerous authors (e.g., Kapfer et al., 2017; Vellend et al., 2013; Verheyen et al., 2018). Legacy plots use a wide variety of sampling methods—from belt transects to $1 \times 1\ m^2$ quadrats to relevés—some of which are permanently monumented but often are not. The relevé method that Sawyer and Thornburgh used in 1969 and that we used in 2015 has potential inherent limitations that are necessary considerations when evaluating temporal changes (please refer to Podani, 2006). By locating plots in what Sawyer and Thornburgh considered representative vegetation, they most probably avoided transition areas, or ecotones, which can result in an oversampling of areas of greater stability. The assumption here is that the relevé method would undersample regions near the edges of species distributions, the very places one would expect the most change. Therefore, the changes we described would be underestimates of the actual changes that occurred across the landscape and therefore some of our conclusions are most likely to be conservative.

Specifically, the unexpectedly slow movement upward in elevation (Table 2; Figure 5), the statistically insignificant changes in cover (Figures 3 and 4), and the seemingly modest change in community composition (Figure 7) may be a function of this sampling bias that is obscuring larger changes. However, we suggest that this bias has a relatively modest impact in our study area compared with others. Our study area is renowned for its high levels of alpha- and beta-diversity (Coleman & Kruckeberg, 1999; Sawyer, 2007; Whittaker, 1960), and almost all our plots represent mixed-conifer forests comprised of multiple species, whereas very few have only a single species. Nonetheless, as with the limitations of using the seven-rank ordinal scale (please refer to *Methods*), this potential sampling bias demonstrates one of the limitations of resampling legacy plot studies. Both biases deserve careful consideration when making conclusions about temporal change in vegetation.

CONCLUSIONS

Our study adds to a growing body of literature describing the resurveying of legacy plots and provides a unique look at multidecadal changes in one of the most species-rich temperate forests in the world. The abrupt curtailment of fire coupled with decades of climate warming and drying in our system are representative of many other forested systems, but the high diversity of conifer species is not. Because of this diversity, no single prediction could suffice for trees in the study area; alternatively it was necessary to treat each life history separately and base predictions on the known effects of shade, drought, and fire. The high diversity of trees was also advantageous in assessing community resistance in species-rich communities and for interpreting changes in forest composition since 1969.

Overall, our results document individualistic species responses and, at the same time, conspicuously consistent directions of decline in response to a warming climate and altered disturbance regimes (Table 5). These responses—represented by modest declines in cover and generally slow movement upslope—are likely to be due to a combination of millennial scale increases in some drought-sensitive species that may be currently at their peak abundance over the last 10,000 years, compounded by more than a century of fire exclusion. However, several changes that we observed portend declines and loss of forest resilience to future drought and disturbance. Most apparent among these declines were canopy reductions of fire-tolerant and drought-tolerant species at low elevations where fire was historically most frequent. Continued loss of these species will decrease resilience to future fires even at higher elevations, where upward migration of more drought-tolerant species may be a key to forest persistence under warmer climatic conditions. In addition, declines in seedlings and sapling suggest lagged responses from recent warming for several high-elevation species that may be on the verge of more widespread and significant declines that would negatively impact regional biodiversity.

Although climate has been the ultimate driver of vegetation change in the region throughout Holocene, paleostudies from Northern California and other parts of the Pacific Northwest implicate fire as an important catalyst of change (Briles et al., 2005; Crausbay et al., 2017; Crawford et al., 2015). Despite notable recent warming over the last half century, the effects of fire suppression are likely to be forestalling many of the anticipated changes based on Holocene dynamics during warming periods. Changes at the community level in diverse assemblages may take long periods of time to manifest in the absence of disturbance to catalyze change, but population level changes, in particular in early life history stages, suggest that shifts have already occurred toward forest conditions that are maladapted to future climate and disturbance (Serra-Diaz et al., 2018). Legacy plots, such as those established by Sawyer and Thornburgh in 1969, will continue providing useful information as remeasurements are made at later dates, including to what degree the Klamath Mountains and other

TABLE 5 Summary of results for 12 conifer species that were observed in a 1969 study and a resurvey of the same plots in 2015 in the Klamath Mountains of California, USA.

Species	Predicted effects of climate change	Predicted effects of fire exclusion	Results
Abies concolor	−	+	Significant increase in canopy cover, especially at middle elevations, and declines in saplings and seedlings; moderate expansion upward (46 m)
Abies lasiocarpa	−	+	Declining cover of all life stages, significant declines in saplings; minimal expansion upward (6 m)
Abies magnifica var. *shastensis*	−	+	Declining cover of all life stages, significant declines in seedlings and saplings; minimal expansion upward (5 m)
Calocedrus decurrens	+	+	Declining cover, significant declines in saplings; greatest expansion upward (70 m)
Picea breweriana	−	+	Declining cover of all life stages, significant decline in saplings; moderate reduction in mean elevation (−25 m) due to decreases at higher elevations
Picea engelmannii	−	+	Declining cover of all life stages, significant decline in saplings; moderate expansion upward (25 m)
Pinus contorta	+	−	Declining cover of all life stages, significant decline in saplings; minimal downward expansion (−5 m)
Pinus lambertiana	+	−	Declining cover of all life stages, significant declines in canopy and saplings; moderate expansion upward (18 m)
Pinus monticola	+	−	Declining cover of all life stages, significant decline in saplings; moderate expansion upward (12 m)
Pinus ponderosa	+	−	Declining cover of all life stages, significant decline in canopy; mean elevation declined (−47 m) due to loss of cover at higher elevations
Pseudotsuga menziesii	−	+	Declining cover of all life stages, significant decline in saplings; moderate expansion upward (24 m)
Tsuga mertensiana	−	+	Declining cover of canopy, significant decline in saplings, increase in seedlings; minimal expansion upward (6 m)

Note: The predicted effects of climate change and fire exclusion are denoted with "+" for an increase in abundance and "−" for a decrease in abundance. These predictions match those shown in Table 1 but are simplified for ease of interpretation. The results shown are derived from incorporating multiple lines of evidence (please refer to the text for details) and include statements about changes in abundance and also changes in elevation.

regions offer climate refugia (Michalak et al., 2020; Thorne et al., 2020).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (DeSiervo & Jules, 2022) are available in Dryad at https://doi.org/10.5061/dryad.9s4mw6mj7.

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SUPPORTING INFORMATION

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

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