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RESEARCH ARTICLE

Increases in understory plant cover and richness persist following restoration treatments in *Pinus ponderosa* forests

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Abstract

1. A combination of forest thinning followed by prescribed burning is widely applied in the western United States to increase ecosystem resistance and resilience to disturbances. Understory plant community responses may be driven by both management treatments and climatic factors. Thus, responses to treatments during a 20-year megadrought have implications for the role of management in fostering adaptive capacity to climate change.
2. We used a network of five sites (600 plots) spanning an environmental gradient in ponderosa pine (*Pinus ponderosa*) forests of the American Southwest, an ecosystem that is broadly distributed and actively managed throughout the western United States. We used repeated long-term monitoring data to quantify plant community responses to treatment 1–5-, 6–10- and >10-year post-implementation. Specifically, we focussed on the effects of treatment and abiotic conditions on native and non-native plant cover and species richness and the proportion of native species with northern (cool-mesic) biogeographic affinities.
3. Overall, thinning and prescribed burning nearly doubled native cover and increased native species richness by about 50% relative to untreated controls. These effects persisted for over a decade after treatment, even under the influence of significant and persistent drought. Cover and richness were also greater on intermediate to wet sites. Finally, native species with northern biogeographic affinities were reduced for up to 5 years after treatment relative to those with southern (warm-xeric) affinities, and in dry years, indicating that both management and interannual climate variability may foster shifts to plant communities that are more resilient to a warming climate.

4. *Synthesis and applications*. In ponderosa pine forests of the American Southwest, tree thinning followed by prescribed burning will generally promote restoration goals of increasing resilience to climate change by enhancing the diversity and abundance of native understory plant species, even during a persistent 20-year megadrought.

KEYWORDS
Arizona, ecological restoration, plant communities, plant diversity, ponderosa pine, treatment effects, understory

1 | INTRODUCTION

In temperate forests, understory plants beneath the tree canopy typically comprise the majority of plant diversity and fulfil many essential ecosystem services and roles (Balandier et al., 2022). In addition to providing food and habitat for animal species, a robust understory can be more resistant to non-native plant invasions (Johnstone et al., 2016; McGlone et al., 2011), promote native fire regimes (Moore et al., 1999) and control tree regeneration (Allen et al., 2002). Forest management and climate change can both alter many aspects of plant communities growing underneath forest canopies, and information relating to these impacts is valuable for informing future management and conservation scenarios.

Low-severity, high-frequency fire is a natural process in many dry forests of the western United States and has long played a valuable role in important processes such as decomposition (Monleon, 1996), nutrient cycling (DeLuca & Sala, 2006), vegetative reproduction and germination of dormant seeds (Kerns & Day, 2018). Following a century of fire exclusion, expanded human populations, increased fuel biomass and continuity and human-altered climates have driven recent increases in fire size and the area burned at high severity, as well as shifts in fire seasonality (Balch et al., 2017; Parks et al., 2023). Such fire regime changes pose threats to the resilience and long-term persistence of many forests in the region and to the species that inhabit them, motivating ecological restoration treatments to reduce future fire severity by removing small trees and other hazardous fuels (Stephens et al., 2018). While this main objective of ecological restoration treatments aligns with that of hazardous fuel reduction treatments (Adams, 2013; Stephens et al., 2012, 2021), restoration treatments also have a wide range of secondary objectives, such as promoting productive and diverse native understory communities. Whereas indigenous practices of burning were widespread throughout North America historically (Long et al., 2021), ecological restoration as a management practice in North American forests has only recently been applied. Restoration treatments also commonly reintroduce, via prescribed burning, a natural fire regime in line with traditional burning practices and historical natural ignition patterns.

Ecological restoration aims to return both resistance (capacity to withstand natural disturbances) and resilience (capacity to recover from natural disturbances) to degraded ecosystems (Lake, 2013). Although tree thinning and prescribed burning are widely applied in western US forests to increase ecological resilience and resistance to natural disturbances, their effects on native understory species are not well understood, particularly across temporal and environmental gradients (but see Jang et al., 2021). Over short time scales (<5 years), a combination of thinning and prescribed fire can increase native plant cover but may have weaker effects on species richness (Strahan et al., 2015). While many native understory species can respond rapidly to management, the responses of others may take many years to unfold (Abella & Springer, 2015; Ash et al., 2017; Lenoir & Svenning, 2015). Likewise, over long time scales, treatment effects may become diminished, necessitating a need for additional management to maintain benefits (Goodwin et al., 2018). Implementation of treatments in diverse physiographic settings will result in a variety of microsites (Davis et al., 2019), which is likely to have a range of impacts on plant communities. Species and community responses differ widely, even in similar forest types, depending on abiotic factors such as moisture availability and topographic position. Such factors are commonly evaluated using tree density, composition and spatial pattern, but understory plant communities are also a critical component of these ecosystems. Depending on several factors such as precipitation, soil exposure and amount of tree canopy removed by treatments, the diversity and abundance of native and non-native understory plants generally increase quickly and persist several years or more due to increased solar radiation and creation of suitable microsites and microclimates (Strahan et al., 2015; Willms et al., 2017), though effects in both the short- and long-term can be highly variable (Jang et al., 2021; Willms et al., 2017). Understanding how gradients affect understory responses to restoration treatments is useful for forest managers in anticipating plant abundance, diversity, productivity and compositional responses that impact understory plant communities (Willms et al., 2017).

Forest management aims of increasing native understory plant community diversity, function and resilience are likely to become increasingly challenging given non-native plant invasions, altered disturbance regimes and increased frequency and severity of drought events under future climate scenarios (De Frenne et al., 2021; Halofsky et al., 2020; Jang et al., 2021). Indeed, shifts in species ranges are expected as the climate becomes more variable and disturbances become more prevalent across large spatial scales (Parks

et al., 2019; Weiskopf et al., 2020). Developing goals for the understory plant community when incorporating restoration prescriptions is challenging due to a lack of historical reference information (Stephens & Fulé, 2005) or knowledge of the long-term effects of a changing climate. With climate change, not only are drought events becoming more common in the western United States, but interannual climate variability is also increasing (Zhang et al., 2021). These climatic influences can heavily impact observed plant responses, such as cover and production (Copeland et al., 2019; Korb & Fulé, 2008). Shifts in drought may hinder species richness, cover or diversity, especially during treatment recovery. Ideally, targeting robust native understory communities, sufficiently resilient to endure periodic stress events, aligns with restoration goals to provide the best chance for recovery from degradation and to improve ecosystem function (Falk et al., 2006). Monitoring long-term understory responses such as plant abundance and diversity will provide insights regarding ecological resilience following restoration treatments.

In this study, we monitored herbaceous and woody understory species responses 1–5, 6–10 and >10 years following thinning and prescribed fire in a multisite network of experimental monitoring plots in Arizona, USA (Figure 1a; Appendix S1). Established between 1997 and 2002, these study sites span the wide environmental gradient that ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) forests inhabit in this region (Figure 1a). Our study period (ca. 2000 to 2020) includes a period of intense and severe drought beginning around the year 2000 (Williams et al., 2020). Because restoration treatments are planned for similar forests covering millions of hectares in the western United States, there are broad implications to understanding understory responses to such treatments. We asked the following research questions: (1) How do tree thinning and subsequent prescribed burning affect understory plant cover and richness, and the proportion of northern affinity (cool-mesic) species across a broad environmental gradient? (2) How are these changes affected by interannual climate and geographic variation in environmental conditions? Our expectations were that plant cover and species richness would increase immediately following treatment, but that persistent drought conditions and waning effects of treatment would drive a decline in cover and richness towards the end of the study period. We also expected that cool-mesic species would decrease in relation to warm-xeric species following treatments due to changes in the micro- and macroenvironment.

2 | MATERIALS AND METHODS

2.1 | Study design and field surveys

Our study area, located in Arizona, USA, included five experimental sites that are a part of the Long-term Ecological Assessment and Restoration Network (LEARN). These five sites employ a consistent experimental design and treatment (Stoddard et al., 2021) (Figure 1a; Tables S1.1 and S1.2). Each of the five study sites contains one or more treated-control unit pairs (approximately 16 ha in size each), for a total of 15 pairs (Table S1.2). Within each pair, the treated units received a restoration treatment that removed small-diameter trees using prescriptions designed to approximate pre-fire-exclusion (i.e. mid-to late-1800s) forest structural patterns (Moore et al., 1999), followed by a low-severity prescribed fire (Stoddard et al., 2021).

We collected monitoring data from 20 plots located within each treatment unit (i.e. 40 plots per treated-control unit pair). Each plot included one 50-m transect, with different protocols used to capture species richness and understory cover. First, we used the point line-intercept method to record all plant species (understory species below 137 cm in height) every 30 cm (totalling 166 points; used to quantify per cent cover) (National Park Service, 1992). We then recorded all species encountered within a 10 × 50 m rectangular 'belt', centred on the transect. Data collection was slated to occur at 1-, 5-, 10- and 20-year post-treatment, but occasionally deviated from the schedule due to logistical constraints (see Table S1.2 for years of data collection). Applicable land management agencies granted permits to conduct fieldwork at all sites and in all years (Tables S1.1 and S1.2). For taxonomic nomenclature, we used www.itis.gov, and we obtained species nativity from the USDA Plants Database (USDA NRCS, 2021). We assigned biogeographic affinities to each of the 475 native taxa recorded in our study following the approach of Harrison and Grace (2007) and others (Stevens et al., 2015, 2019) (Appendix S5), ultimately distinguishing between those with a northern affinity where evolutionary climates (and presumably modern environmental preferences) were cooler or more mesic (cool-mesic) versus those with warmer or more xeric affinities (warm-xeric).

2.2 | Data analysis

To answer our research questions, we used two complementary analytical methods—Cohen's *d* effect size analyses and generalized linear mixed models (GLMMs). We used Cohen's *d*, a common method of calculating standardized effect sizes of treatments (Cohen, 1988; Lin & Aloe, 2020), to describe the coarse-scale (i.e. unit-level) impacts of treatment on native, non-native and proportion of northern affinity species cover and richness and how impacts changed over time. Next, we used GLMMs to quantify the fine-scale (i.e. plot-level) effects of treatment and environmental drivers on understory communities. In our GLMMs, the response variables included total understory species cover, richness and the proportion of northern affinity species. We treated understory cover as a binomial response derived from point line-intercept transects, which gave the proportion of a plot with any understory cover in a given survey year (i.e. n successes = number of plant 'hits' on a transect; n trials = 166). To quantify species richness, we tallied the number of unique species found on belt transects within each plot and survey year, for which we used a Poisson error structure. To describe the proportion of cool-mesic species on each plot and year, we determined the proportion of the vegetated points (i.e. n trials) in point line-intercept transects that had a species with a northern affinity in the top plant strata (i.e. n successes), which we treated as a binomial response.

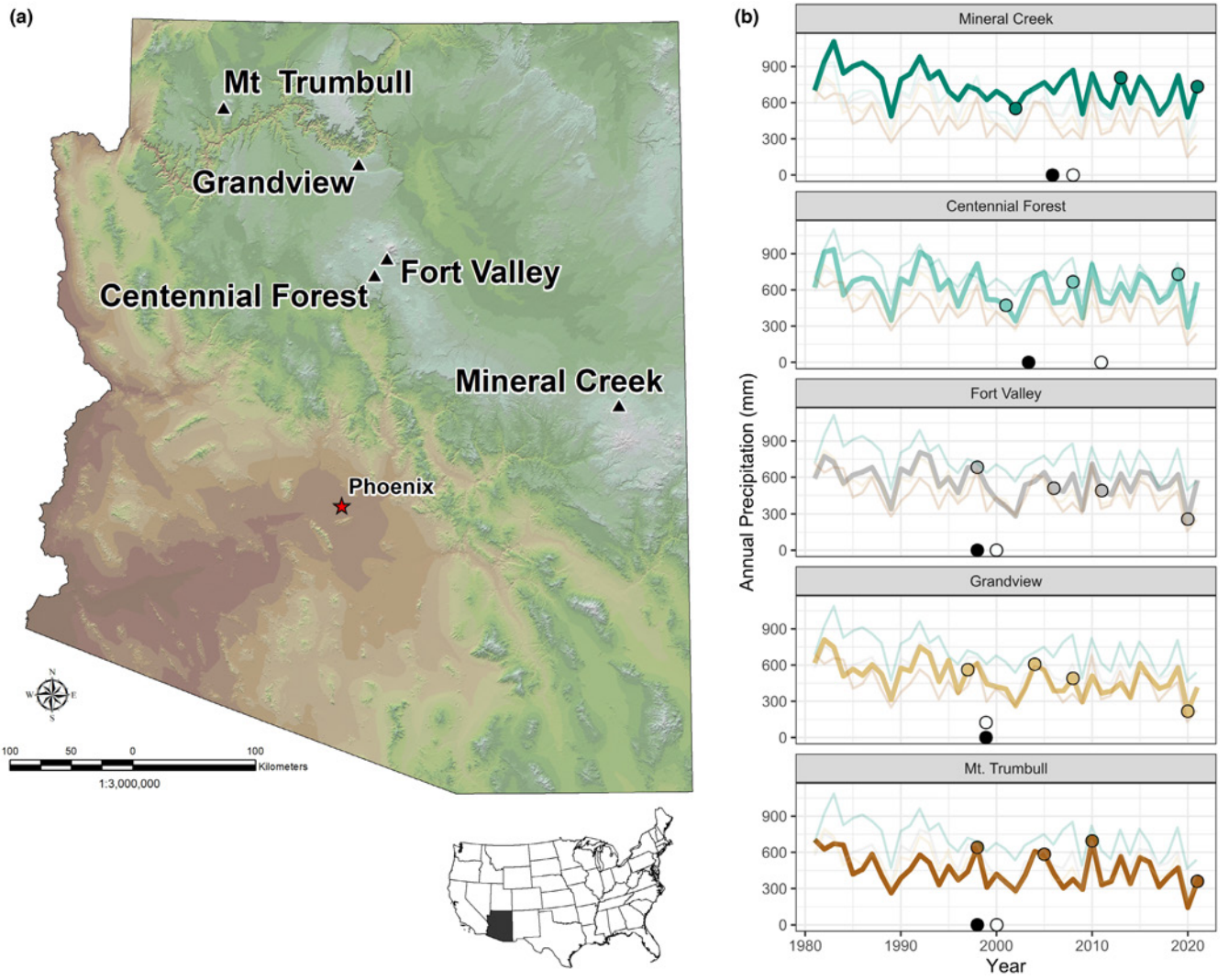

FIGURE 1 (a) Study sites in northern and eastern Arizona, USA, spanning *Pinus ponderosa* forests with experimental thinning and burning treatments and (b) total annual precipitation by site from 1981 to 2021. Background colours in (a) indicate topographic relief, with white and darker green representing higher elevations that receive more precipitation than the surrounding areas. Precipitation panels in (b) are ordered from highest (top) to lowest (bottom) mean annual precipitation. Shaded circles along precipitation lines denote years of data collection. At the bottom of each panel in (b), black circles mark the initial years of thinning, and white circles mark the initial years of burning at a site.

To model each response variable in GLMMs, we used plot-level (i.e. 30-m spatial resolution) covariates of average climatic water deficit (CWD) from 1991 to 2020, annual CWD in the sampling year (scaled to *z*-scores relative to the long-term mean and standard deviation at a plot) and topographic position index (i.e. TPI; an indicator of topographic exposure of a plot relative to its surroundings), as well as the unit-level covariate of treatment (i.e. untreated, 1–5-year post-treatment, 6–10-year post-treatment, or >10-year post-treatment) (Appendix S2). In each model, we also included a random intercept term of plot to account for repeated sampling within a plot over time, and we included a Matérn spatial correlation term (Rousset & Ferdy, 2014) to account for spatial dependence among adjacent plots. We tested for potential interactions between average and annual CWD, as well as nonlinear effects of CWD on each response. We selected final covariates for each model as the combination of terms that minimized the sample size corrected variant of Akaike's Information Criterion (AICc) without evidence of overfitting, but we also present models with partial support (ΔAICc <4) in Appendix S4. Additional supporting information for analyses can be found in Appendices S2–S4.

3 | RESULTS

3.1 | Cohen's d effect sizes

Treated units showed general increases in native and non-native cover and richness compared with paired control units, while also exhibiting reductions in the proportional cover and richness of native northern affinity species. Increases in both native and

non-native species cover due to treatment persisted for more than 10 years after thinning and burning were implemented (Figure 2). Native cover had a greater positive response to treatment than did non-native cover, except during the 1–5-year post-treatment period. At the drier sites (particularly Mt. Trumbull), treatments had a greater stimulatory effect on non-native cover than at the other wetter sites. Treatments reduced the proportional cover of native northern affinity species for up to 10 years. Like cover, the richness of both native and non-native species was greatest in treated areas for over 10 years. Additionally, the proportion of native species with a northern affinity was also reduced following treatments for over 10 years (Figure 2).

3.2 | Generalized linear mixed models

Plot-level vegetation cover was best predicted using a combination of treatment group, 30-year average CWD of a plot and annual CWD during the measurement year, with no two-way interactions (Figure 3) (ΔAICc = 1.02 from the next best model; Table S4.1). At 1–5-years post-treatment, treated areas had twice the amount of total plant cover when compared to untreated areas, though this effect diminished somewhat with time since treatment (Figure 3a). Areas of intermediate moisture availability (i.e. average CWD values 150–250 mm) and wet years (i.e. annual CWD *Z*-scores <0) were associated with the greatest plant cover.

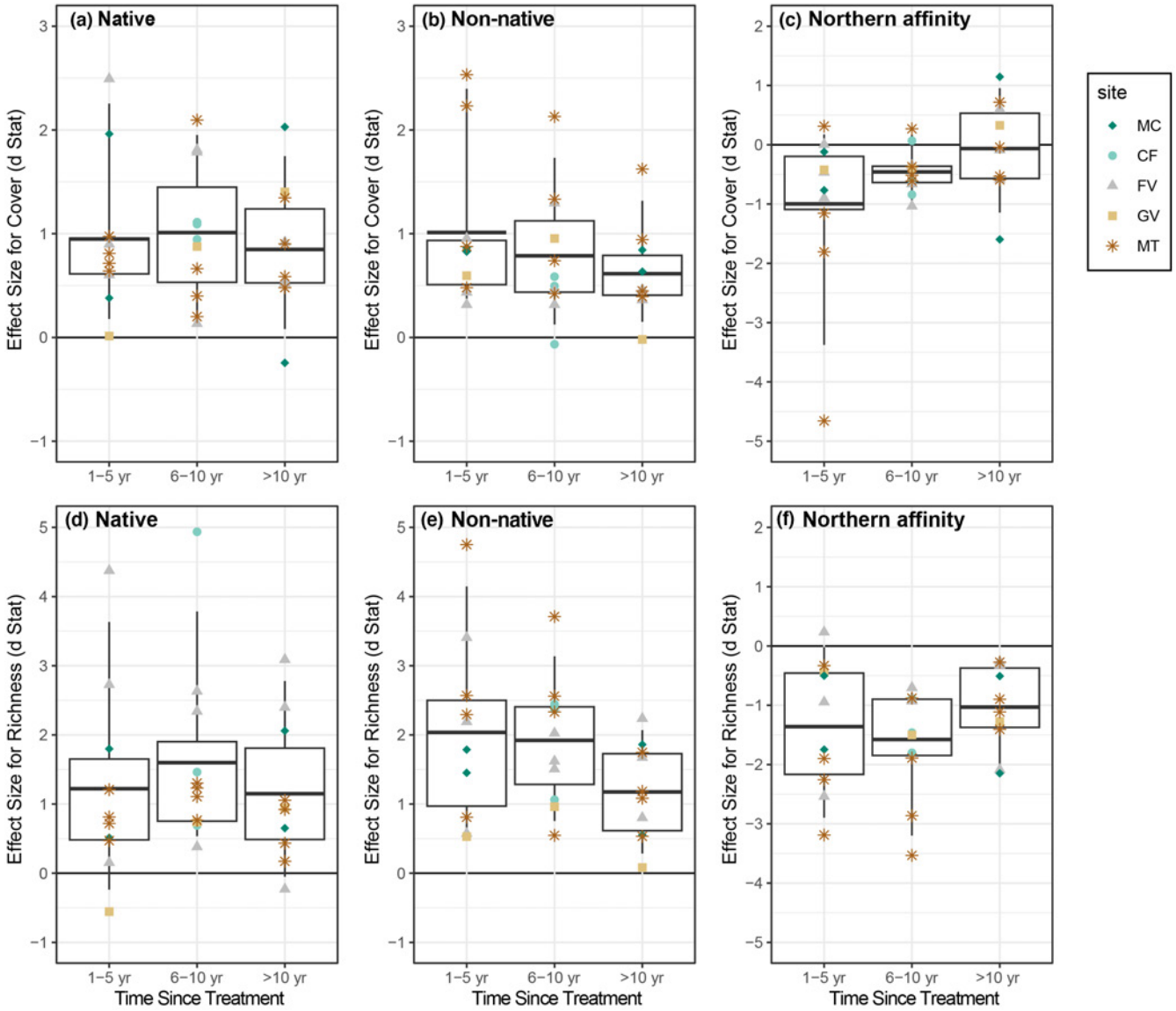

FIGURE 2 Cohen's *d* effect size results for both cover (a–c) and richness (d–f). Box plots represent 25th and 75th percentiles, whiskers represent 5th and 95th percentiles, and solid lines represent mean effect sizes. Points show values of treatment–control pairs within each site (Centennial Forest = CF; Fort Valley = FV; Grandview = GV; Mineral Creek = MC; Mt. Trumbull = MT). If most of the box and whisker do not overlap the 0 line, it indicates a consistent difference between paired treated and untreated units, with positive values indicating an increase in a variable (i.e. cover or richness) due to treatment, and negative values indicating a decrease. Northern affinity is represented by the proportion of species assigned to that biogeographical affinity.

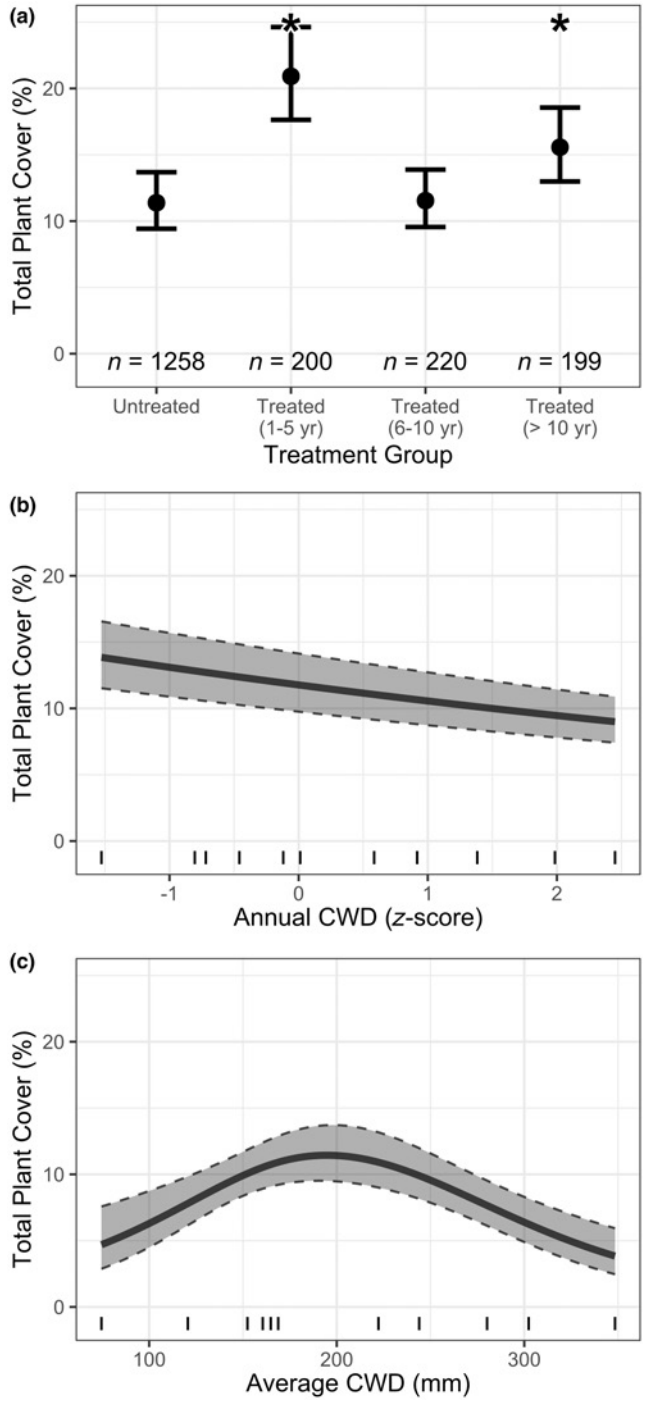

FIGURE 3 Effects of predictors included in the top generalized linear mixed model of vegetation cover in evidence-based forest restoration treatments across five *Pinus ponderosa* study sites in Arizona, USA. Panels show the marginal effects of treatment (a), interannual climate (b) and average climate (c) on the response variable, assuming mean values for the other predictors (or the 'untreated' group in [b]) and of random effect terms included in the final model. Error bars (a) and grey ribbons (b, c) give ± one standard error of prediction. In (a), (*) indicates significant differences ($p < 0.05$) between a treatment group and untreated controls based on a Wald test. The number of plot sampling years included in each group is given in (a), while black tick marks in (b) give decile values showing the distribution of each predictor in the data. CWD, climatic water deficit.

Plant species richness within a plot was best predicted using a combination of treatment group, TPI, average CWD and annual CWD, and a two-way interaction between average and annual CWD (ΔAICc = 0.65 from the next best model; Table S4.3). Species richness was nearly 50% higher in treated areas, with effects persisting for over 10 years following combined thinning and initial burning (Figure 4a). Valley bottoms (i.e. TPI < −10) typically had greater species richness than did drier ridgetops (i.e. TPI > 10) (Figure 4b). Wet sites (i.e. average CWD < 150) and dry years (i.e. annual CWD > 0) also typically had the greatest plant species richness (Figure 4c). The interaction term between average and annual CWD indicated that the positive effects of dry years on richness were most evident on wet sites (Figure 4c).

The proportion of native plant species with northern biogeographic affinities (i.e. cool-mesic species) was best predicted by a combination of treatment and annual CWD with no retained interactions (ΔAICc = 0.97 from the next best model; Table S4.5). Overall, treated areas had a reduced dominance of northern species relative to controls, with the strongest effects within 5 years of treatment (Figure 5a). Annual CWD was negatively associated with northern species dominance, indicating that wet years were associated with increases in northern species.

4 | DISCUSSION

4.1 | How do combined tree thinning and burning treatments affect understory plant cover and richness, and proportion of native northern affinity species?

Our long-term experiment spanning a range of environmental conditions indicated that thinning followed by burning in dry forests can increase native understory plant cover in the presence of changing climatic conditions and persistent drought (Figures 1 and 2). Moreover, while increases in plant cover following removal of tree canopy have been widely documented in the initial years after disturbance during periods of favourable precipitation (Strahan et al., 2015; Thomas & Waring, 2015), our study illustrated that increases can be maintained during a 20-year megadrought. Sites with intermediate moisture availability and wet years were associated with the greatest increases, and native plant cover and richness were consistently greater in treated areas compared with controls during a period of extended drought. While perennial forbs comprise the bulk of species richness in these systems following treatments, the perennial graminoids are most responsible for increases in cover, particularly the C_3 species (Strahan et al., 2015). Our findings indicated that treatments, when compared to the controls, provided resilience to the plant community, primarily in the form of increased cover, during a climatic period considered to be a megadrought in the Southwest.

Moreover, all five sites showed native richness increases due to thinning and burning treatments (Figure 2). Since annual species often exhibit seed dormancy during drought (LaForgia et al., 2018),

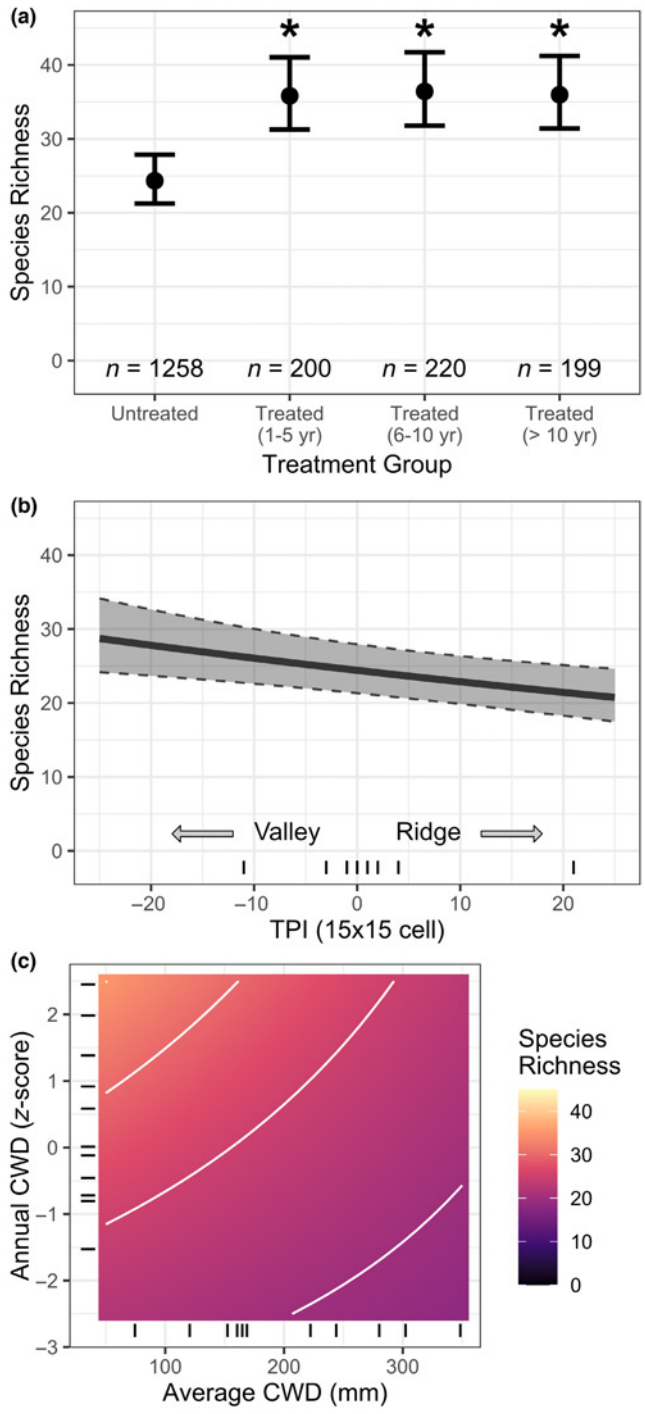

FIGURE 4 Effects of predictors included in the top generalized linear mixed model of plant species richness in evidence-based forest restoration treatments across five *Pinus ponderosa* study sites in Arizona, USA. Panels show the marginal effects of treatment group (a), topographic position (b), or the interactive effect of average and interannual climate (c), on the response variable, assuming mean values (or the 'untreated' group in [b, c]) for the other predictors and of random effect terms included in the final model. In (a), error bars (a) give ±1 standard error of prediction, and (*) indicates significant differences ($p < 0.05$) between a treatment group and untreated controls based on a Wald test. In (b), ribbon/dashed lines give ±1 standard error of prediction. In (c), white contours are spaced at increments of five species. The number of plot sampling years included in each group is given in (a), while black tick marks in (b, c) give decile values showing the distribution of each predictor in the data. CWD, climatic water deficit.

and some perennial species remain dormant below-ground during dry periods (Gremer et al., 2012), this trend suggested that decreased tree competition can enhance survival for some understory plant species through nearly two decades of drought. Other studies have shown that understory species richness responses to fuel reduction treatments in western US forests can be highly variable or insignificant, depending on the type of treatment and length of time following treatments (Willms et al., 2017). The decline in the proportion of cool-mesic species in our study also points to a need for continued monitoring of species adapted to low-light environments that may have been more common prior to treatments.

Although native cover and richness increased following treatments in our study, non-native cover and richness also demonstrated increases. Non-native species, which tend to efficiently capitalize on available resources (Theoharides & Dukes, 2007), responded more quickly to treatments than native species, but natives tended to maintain gains over a longer period. The responses of both native and non-native species, when compared to controls, were strongest at some of the drier sites, particularly at Mt. Trumbull. This site had a preponderance of invasive cheatgrass (*Bromus tectorum*), which is common in warm, dry areas in the Southwest and Great Basin. Propagule pressure is high at Mt. Trumbull (McGlone et al., 2011), even before treatments, and its isolated location as a higher elevation forested island in the middle of shrub- and grasslands allows for little inflow of native seeds from similar habitats to augment the existing native plant community and provide resilience to invasion. A major objective of restoration projects is creating resilience to non-native plant invasions by maintaining a healthy and diverse native understory (McGlone et al., 2011). However, drought has been shown to suppress seedling establishment of some non-native species, with potential interactive effects between drought and disturbance (Orbán et al., 2021). McGlone et al. (2011) posited that the inability of *B. tectorum* to invade extant patches of native-dominated understory at Mt. Trumbull even in the presence of high cheatgrass propagule pressure and disturbance may be due, in part, to decreased levels of winter precipitation during the long-term drought. Continued monitoring during times of favourable precipitation would be valuable in tracking changes in non-native establishment. While cover of non-natives was relatively low at all five sites, the drier sites may be more vulnerable to increases in non-native species.

4.2 | How are these changes affected by interannual climate and geographic variation in environmental conditions?

Based on our models, the best abiotic predictors of plant cover were average and annual CWD, with the lowest plant cover observed in dry years and away from valley bottoms and drainages. Treatment effects

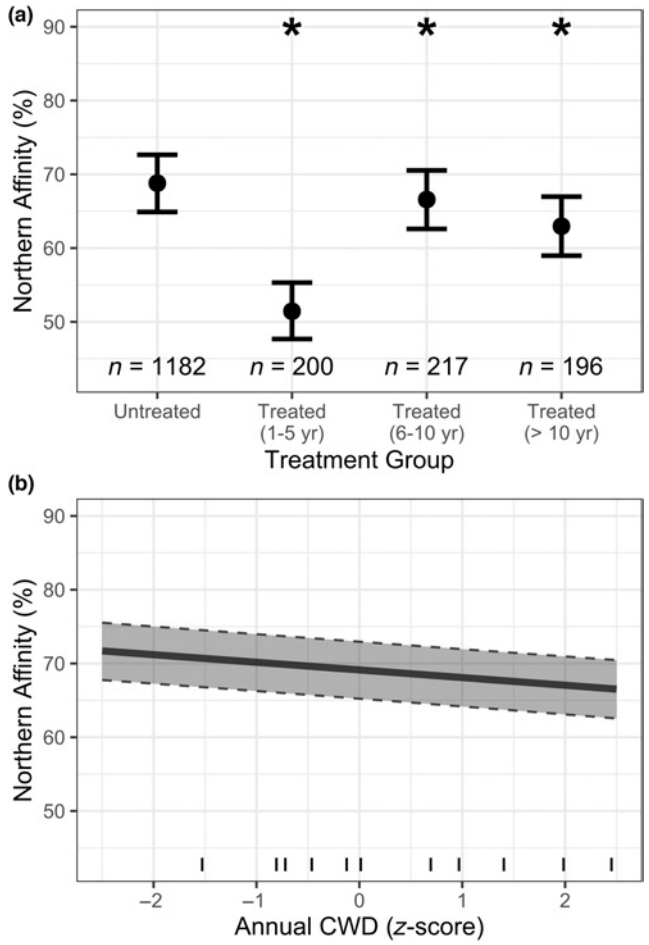

FIGURE 5 Effects of predictors included in the generalized linear mixed model of dominance by plant species with northern biogeographic affinities in evidence-based forest restoration treatments across five *Pinus ponderosa* study sites in Arizona, USA. Panels show the marginal effects of individual predictors on the response variable, assuming mean values for the other predictors (or the 'untreated' group in [b]) and of random effect terms included in the final model. Error bars (a) and ribbon/dashed lines (b) give ±1 standard error of prediction. The number of plot sampling years included in each group is given in (a), while black tick marks in (b) give decile values showing the distribution of each predictor in the data. CWD, climatic water deficit.

prevailed over climate even during particularly droughty years. Since CWD and other abiotic factors generally cannot be manipulated at a large scale, tree thinning and prescribed burning are some of the few management practices available to increase plant cover and species richness. The native understory communities at our sites demonstrated initial post-treatment decreases in species with a northern biogeographic affinity. The proportion of species with a northern affinity began to approach pretreatment levels over time, but GLMMs indicated that they remained significantly different from controls through the course of the study (Figure 5). This indicated some 'thermophilization' of the community (i.e. an increase in species that prefer warmer, drier conditions) for nearly 20-year post-treatment (Figures 2 and 5). Other studies have found similar community changes following high-severity wildfire (Stevens et al., 2015, 2019). Stoddard et al. (2011) showed that thermophilization can be due to increases in ruderal and disturbance-dependent species emerging after treatments. We suggest that treatments in our study led to plant communities more reflective of a frequent-fire environment that was likely present prior to fire exclusion (Laughlin et al., 2011). In contrast, contemporary coniferous forests can be dominated by less drought-adapted species that can only prosper under dense canopies where the microclimate is cooler and wetter (Laughlin et al., 2011). Thus, forest restoration treatments appear to increase and facilitate establishment and/or growth of drought-tolerant species (e.g. C_4 grasses). However, Laughlin et al. (2008) found that *Muhlenbergia montana* (mountain muhly), a C_4 grass, was negatively affected by repeated prescribed fires that occurred in the fall. More work is needed to examine the long-term effects of treatments on individual species.

Ponderosa pine forests across the study area were historically open and characterized by native perennial grasses and forbs that carried frequent (i.e. <30-year intervals) surface fires (Moore et al., 1999). Due to overgrazing, fire suppression and associated increases in tree density, herbaceous cover has typically declined in these forests (Moore et al., 1999). The combination of tree thinning and burning can increase available light, moisture and nutrients in the short term (Kaye & Hart, 1998), providing a mosaic of conditions favourable for stimulating growth and reproduction of plant species adapted to high light conditions. Initial disturbances also create a range of microsite conditions and trigger germination cues for seeds stored in the soil (Korb et al., 2005). In the present study, fire-adapted graminoids and prolific seed-producing species, such as members of the Asteraceae family, began to dominate the plant communities in these systems towards the end of the study period, with ruderal species becoming less prevalent. While thinning provides long-term conditions favourable for understory plant development (McGlone, Springer, & Laughlin, 2009), subsequent burning creates bare soil necessary for successful seed germination of both herbaceous plants and trees, particularly in areas where heavy accumulations of organic matter create a barrier. Perennial grasses provide competition with tree seedlings. Thus, exposed mineral soil is important for pine regeneration. Repeated burning keeps some woody species in check and provides a mosaic of microsite conditions to sustain higher plant diversity. However, frequent, repeated burning can reduce biomass and potentially favour resilient sprouting species (Guiterman et al., 2018). Implementation of restoration treatments in our study allowed for the reestablishment of a robust perennial grass understory across the study network. This is significant since the network included a range of conditions from more mesic (e.g. Mineral Creek) to drier sites that are near the transition between pinyon–juniper woodlands and ponderosa pine forests (Mt. Trumbull and Grandview) (McGlone, Springer, & Covington, 2009). Although grasses constituted the majority of cover, the contemporary herbaceous community was also defined by a diverse, though less abundant, component of both annual and perennial forbs.

The main limitation of our study was a lack of burning-only and thinning-only treatments to tease out the influence of the individual

treatment effects. Our study design was also built around the concept of repeat prescribed burning at regular intervals to mimic frequent low-intensity fire, with thinning activities generally only occurring at the onset of a project. However, the ability to burn at regular intervals is dependent on social and political factors, as well as conducive weather. Continued monitoring will be useful in determining how individual species, including invasive non-natives, respond to repeat burning, particularly frequency and seasonal variation. In addition, due to the size of the treatment areas, excluding livestock was not feasible because of cost and existing federal grazing allotments, making it difficult to impossible to determine whether current livestock grazing was having an influence. However, CWD was used to test for drought effects, and the overall design provides a realistic test of the effects of forest restoration treatments on a landscape scale in areas that are managed with active livestock grazing, which is representative of most public lands in the western United States. Additional research could examine individual species responses to restoration treatments to increase our understanding of which species will predominate following treatment, and which species drive compositional changes. Such research would also determine species that require alternative conservation efforts. Lastly, research to examine the effects of deferring livestock grazing for various periods of time after restoration treatment implementation would be useful.

Millions of hectares of fire-adapted forests in the western United States are currently slated for ecological restoration and hazardous fuel treatments over the coming decades, and these treatments are increasingly being studied and incorporated globally (Keenan et al., 2021; Rabin et al., 2022). Information gained from the effects of prescribed burning and variable levels of tree thinning is valuable to resource managers when determining whether treatments are meeting planned management objectives. Many factors, in addition to thinning and burning, influence the amount of cover that is available for habitat, grazing or fuel for fires. These include CWD and topography, as well as climate and grazing ungulates, which are difficult if not impossible to manipulate on a landscape scale. Though plant communities varied across abiotic gradients, our study demonstrated that combined thinning and burning can increase plant cover and richness and increase resilience of the forest understory to climate change for up to two decades following restoration treatments, providing useful information for future management and conservation planning.

AUTHOR CONTRIBUTIONS

Judith D. Springer, Michael T. Stoddard, Kyle C. Rodman, David W. Huffman, Paula J. Fornwalt, Daniel C. Laughlin, Peter Z. Fulé, Margaret M. Moore, Becky K. Kerns, Jens T. Stevens, Julie E. Korb and Sara Souther conceived the ideas and designed methodology; Judith D. Springer, Michael T. Stoddard, Rory J. Pedersen, Daniel C. Laughlin, Christopher M. McGlone, Mark M. Daniels and Julie E. Korb collected the data; Judith S. Springer, Michael T. Stoddard and Kyle C. Rodman analysed the data; Judith D. Springer, Michael T. Stoddard, Kyle C. Rodman and Paula J. Fornwalt led the writing of the initial draft. All authors contributed to the writing and editing of drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare that are relevant to the content of this article.

DATA AVAILABILITY STATEMENT

Data, R code and model outputs are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.rv15dv4dq (Springer et al., 2023).

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SUPPORTING INFORMATION

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

Appendix S1: Detailed descriptions of study sites and field data collection methods.

Appendix S2: Detailed description of analytical methods.

Appendix S3: Descriptive plots.

Appendix S4: Model selection results and summaries of final generalized linear mixed models.

Appendix S5: Summary of plant species included in this study.

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