



Decreased snowpack and warmer temperatures reduce the negative effects of interspecific competitors on regenerating conifers

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Abstract

The persistence and distribution of species under changing climates can be affected by both direct effects of the environment and indirect effects via biotic interactions. However, the relative importance of direct and indirect climate effects on recruitment stages is poorly understood. We conducted a manipulative experiment to test the multiway interaction of direct and competition-mediated effects of climate change on vegetation dynamics. Following stand-replacing fire in California mixed-conifer forest, we seeded two conifer species, *Pinus ponderosa* and *Abies concolor*, in two consecutive years, one relatively normal and the other with an unusually wet and snowy winter followed by a hot summer. We additionally manipulated snow amount and competitive environment for both years. We found the effects of the snowpack treatment were contingent upon other abiotic factors (year of seeding) and biotic factors (shrub competition). Under ambient snowpack, shrubs reduced recruitment of *P. ponderosa* seedlings, but this negative effect disappeared with reduced snowpack. Additionally, the effects of shrubs on seedlings differed between cohorts and by life stage. In a warmer future, decreased snowpack may increase seedling emergence, but hotter and drier summers will decrease seedling survival; the effects of shrubs on conifers may become less negative as temperatures increase.

Keywords Climate change · Fire · Interannual variation · *Pinus ponderosa* · Year effects

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Climate change has the potential to shift the balance between species regenerating after fire. We experimentally tested the effects of climate change on post-fire regeneration and shifts in species interactions. We found that the effects of climate manipulation on conifer regeneration differ depending on year of planting and interactions with neighboring plants. This demonstrates the importance of experiments initiated across multiple years in teasing apart abiotic and biotic components of climate change impacts.

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Introduction

As future climates shift further from historical norms, plant communities will be subject to a variety of changing stressors. These changes will include direct effects of changes in weather patterns and indirect biotic effects through changing interactions with other species. Warming temperatures worldwide are predicted to result in decreased snowpack and earlier snowmelt in mountain areas (Barnett et al. 2005). Changes in snowpack and snowmelt, combined with higher temperatures year-round, can influence population mortality (Allen et al. 2010; Young et al. 2017), species distributions (Kelly and Goulden 2008), and community composition (Allen and Breshears 1998). In the southwest US, recent years have already included a historically unprecedented multi-year drought event with high temperatures and low snowpack (AghaKouchak et al. 2014; Diffenbaugh et al. 2015); forecasts predict further warming and increases in aridity (Cook et al. 2015). However, it remains unclear how climate change will impact vegetation through combined direct and indirect effects, particularly during recruitment stages.

Recognition of the role of contingency and multiway interactions in community ecology and regeneration is increasingly becoming the norm (Chase 2003; Chamberlain et al. 2014; Young et al. 2016). One such contingency is “year effects”—the dependence of recruitment and subsequent community trajectories on conditions in the years of plant establishment and community assembly (Vaughn and Young 2010). In particular, increasing attention has been paid to the weather patterns in the years immediately following disturbance, which may promote or inhibit recruitment of different species according to their regeneration niches (MacDougall et al. 2008; Stuble et al. 2017a). Environmental conditions during the regeneration stage may have profound consequences for population persistence under future climate conditions (Jackson and Betancourt 2009), both directly and indirectly through biotic interactions (HilleRisLambers et al. 2013). The role of initial conditions during regeneration may be particularly important in biological systems that are shaped by high-severity disturbances, either for natural disturbances (e.g., treefall gaps, fire, flooding) or anthropogenic ones (abandoned agriculture, logging, planting of degraded areas).

Semiarid mixed-conifer forests in the western US are subject to disturbance by fires, and post-fire regeneration is a vital stage of recruitment for many species (Safford and Stevens 2017). Species with high post-fire recruitment include conifers that disperse seed to the site, “sprouter” shrubs and hardwoods that coppice from surviving below-ground root tissue, and “seeder” shrubs and herbaceous species with seed banks that survive the fire and are triggered to germinate by post-fire conditions. Initial differences in post-fire recruitment can have long-lasting effects on tree density and community structure (Savage and Mast 2005; Santala et al. 2019). Therefore, factors that affect post-fire recruitment may have persistent consequences.

A variety of observational and modeling evidence indicates that post-fire weather patterns are likely to affect initial recruitment and long-term population and community structure of conifer species (Gray et al. 2005; Donato et al. 2016; Liang et al. 2016; Rother and Veblen 2016; Young et al. 2018). In general, these approaches have indicated that mesic sites or wetter years are more likely to support conifer recruitment than xeric sites or drier years. The effects of post-fire weather on conifer recruitment may also depend on how limited a system is by water or energy and growing season length. Systems with high snowpack and short growing seasons are likely to be positively affected by warming and reduced snowpack. In contrast, recruitment in those systems that are more water-limited and have longer growing seasons is likely to be negatively affected by warming and reduced snowpack. Responses to post-fire weather can also be species specific, with some species but not others responding to differences in post-fire weather factors (Harvey et al.

2016; Urza and Sibold 2017; Young et al. 2018). Only one experiment in western US mixed-conifer forests has directly manipulated weather to test its impact on conifer seedling recruitment after disturbance, but not in burned areas, and not in combination with other factors such as the competitive environment (Rother et al. 2015). While large-scale observational analyses are vital for distilling mean effects that are consistent across space and time, focused experiments can discriminate the variation in these patterns, including context- and species-dependent outcomes.

To understand the effects that climate changes will have on forest communities—and potentially reconcile contrasting observations among previous studies of tree–climate relationships—it may be important to consider the impacts of changing interactions with other species (HilleRisLambers et al. 2013). Observational and modeling studies in western US mixed-conifer forests suggest that differences in post-fire weather may shift the balance between conifers and other functional groups, with areas of low conifer recruitment often associated with higher regeneration of other vegetation (Welch et al. 2016). In extreme cases, burned areas with low conifer regeneration can exhibit conversion to shrublands or grasslands (Savage and Mast 2005; Dodson and Root 2013; Donato et al. 2016; Welch et al. 2016; Tepley et al. 2017). These negative correlations between conifer recruitment and dense shrub cover are often attributed to competitive interactions between shrubs and conifers, and the traditional view of conifer–shrub interactions is a competitive one (Shainsky and Radosevich 1986; Putz and Canham 1992; Royo and Carson 2006). Consequently, broad shrub control to promote tree recruitment is a standard silvicultural treatment after fire (McDonald and Everest 1996; Wagner et al. 2006; McDonald and Fiddler 2010). However, studies of conifer–shrub interactions (primarily in unburned settings) have also found evidence of facilitation through canopy shading decreasing heat loading, evaporation, or transpiration (Barbour et al. 1998; Kitzberger et al. 2000; Gómez-Aparicio et al. 2005; Sthultz et al. 2007; Holmgren et al. 2011) or through below-ground interactions (Gómez-Aparicio et al. 2005; Oakley et al. 2006). These variable results raise the question of how shrub and conifer interactions vary with abiotic context, and in particular how shrubs influence post-fire conifer recruitment in a changing climate.

The stress-gradient hypothesis predicts that interactions are more likely to be facilitative in harsh environments if one species can ameliorate the physical stress experienced by another (Bertness and Callaway 1994). However, this depends on whether the dominant stress factor is also a shared limiting resource (Maestre et al. 2009). If the dominant stress factor for conifer seedlings in post-fire conditions is a non-resource factor (e.g., heat stress or evaporative demand), we would expect a more positive interaction between shrubs and conifers in more xeric conditions.

However, if the dominant stress factor is a limiting resource (such as soil moisture availability) for which species are competing, we would expect a more negative interaction between conifers and shrubs in more xeric conditions. Observational evidence of how conifer–shrub interactions vary by environment is limited and somewhat contradictory: conversion of burned forest to shrubland occurs more often at xeric sites (Dodson and Root 2013; Donato et al. 2016), but a meta-analysis (of studies in unburned settings) found stronger facilitation of conifer seedlings by nurse shrubs in more xeric sites (Gómez-Aparicio et al. 2004). Experimental evidence is needed to determine how post-fire interactions between shrubs and conifer seedlings varies with abiotic context, whether these interactions vary by conifer demographic stage, and what the consequences of these interactions may be for conifer recruitment in changing climates.

In addition to direct experimental manipulations, carrying out field experiments across multiple years can combine the controlled setting of an experiment with natural temporal variation in weather conditions (Vaughn and Young 2010). Identifying these types of variation can highlight opportunities for establishment that would be masked by approaches that only consider long-term averages (Serra-Diaz et al. 2015), and they have important implications for analyses of population dynamics, community assembly, species distribution models, and landscape models. These year effects can give insights into future climate-driven patterns, particularly if experiments include years outside the normal range of variation that may be similar to projected future non-analog climates (Stuble et al. 2017b).

In this study, we monitored conifer seed and seedling performance over multiple years in an experiment at a naturally burned site. Our study system in mid-elevation Sierra mixed-conifer experiences long, dry summers and is generally considered to be water limited rather than energy limited (Safford and Stevens 2017). We directly placed seeds into our plots to control for dispersal factors, and manipulated snow and shrub cover, important abiotic and biotic factors which are known to influence post-fire recruitment in these forests. This allowed us to test the following hypotheses:

(H1) Reduced snowpack (i.e., lower moisture availability and longer dry season) would have negative effects on conifer recruitment.

(H2) If weather conditions differed strongly between years, we would observe “year effects” (specifically, differing recruitment and the treatment effects depending on year of cohort planting). For example, in a drier year, we would expect lower recruitment (due to water limitation) and a weaker negative effect of snowpack reduction (because there is less snow to remove).

(H3) Shrub presence would have an overall negative effect on conifer recruitment; however, consistent with

the stress-gradient hypothesis, interactions with shrubs would be less negative in more stressful conditions. If reduced snowpack created more stressful abiotic conditions (as predicted in H1), the biotic interactions with shrubs would be less negative in this treatment. Similarly, interactions with shrubs would be less negative in the more abiotically stressful year (H2).

(H4) The effects of (a) reduced snowpack and (b) shrub interactions on conifer early life stages would differ by conifer species according to their drought and shade tolerance.

Methods

Study site

This study took place in California mixed-conifer forest, which is one of the most common and widely distributed forest types in California (North et al. 2016). This study was conducted in the Eldorado National Forest, El Dorado County, CA, USA (38.921, – 120.517; elevation 1450 m) within the perimeter of the King Fire, which burned in September 2014. Climate data for the site were extracted using bilinear interpolation from monthly ~4-km-resolution PRISM grids (PRISM Climate Group 2016) for the period from 1981 through 2016, and normal climate was computed for the 30-year period from 1981 through 2010. On average, the site receives 1460 mm of precipitation annually (10th–90th percentile range 989–2187 mm), of which over 90% falls during the wet, cold season from October to April, and < 10% falls during the hot, dry season. At the nearby Blodgett Forest Research Station (15 km away; 1300 m elevation), mean annual snowfall is 2440 mm and constitutes an average of 22% of total precipitation (Stevens and Latimer 2015). The normal (1981–2010) January mean temperature at the study site is 5° C (normal January daily minimum: 0° C) and the normal July mean temperature is 22° C (normal July daily maximum: 29° C).

The most common canopy species in California mixed-conifer forest are the yellow pines (*Pinus ponderosa* and *P. jeffreyi*), which are relatively shade intolerant and dominate in xeric and more open sites, where soils are poor and/or where low-to-moderate-severity fires dominate the disturbance regime. These are intermixed with more shade-tolerant but less fire-tolerant conifer species, including white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), especially in more mesic sites, higher elevation sites, and/or areas where fire has been excluded for decades. Also common is the black oak (*Quercus kelloggii*) which often reaches canopy heights and can resprout after fire (Safford and Stevens 2017). Our study site was selected to be relatively flat and with high

initial shrub regeneration; shrub species in the site include *Chamaebatia foliolosa*, *Ceanothus cuneatus*, *C. integrerrimus*, *Arctostaphylos viscida*, and *A. patula*.

Our study focused on two locally dominant native conifer species: *P. ponderosa*, which is usually considered relatively drought tolerant and shade intolerant, and *A. concolor*, which is considered highly shade tolerant but drought intolerant (Safford and Stevens 2017). *P. ponderosa* is found in a geographical range that spans the western US, southwest Canada, and northern Mexico; in the Sierra Nevada, the species' elevational range is approximately 300–2100 m. *A. concolor*'s local elevational distribution is slightly higher, from 800 to 2500 m, and the species range includes the southern Rockies, the southwestern US, and Pacific coastal and interior forests from southern Oregon to Baja California. This study was conducted near the middle of the elevational and geographical ranges of both species. Due to their divergent ecological tolerances, *P. ponderosa* behaves as an earlier successional species, successfully recruiting in hot or dry and high-light conditions after disturbance, whereas *A. concolor* more often recruits later in the successional process, with high survival even under densely shaded canopies of trees or sub-canopies of shrub species (Safford and Stevens 2017).

Experimental manipulations

We conducted a manipulative field experiment to investigate how conifer recruitment was influenced by winter precipitation and shrub presence. We had a total of four treatments combinations (precipitation reduction alone, shrub removal alone, precipitation reduction and shrub removal together, and control). Each treatment plot was 2 m × 4 m, separated by a minimum 1 m buffer. Shrubs in the shrub removal treatment plots were hand-clipped to ground level and treated with cut-stump application of 40% glyphosate herbicide (Fig. 1a). A modified version of a rain-out shelter was used to manipulate winter snowpack. Each year, shelter treatments were applied in November and removed in April, with no shelters during the warm season. Shelters were 2 m × 4 m in area to cover the whole treatment plot, and 1.3 m tall at the center, with sloping sides to shed snow. They were constructed from 2.5-cm PVC pipe, with 20-gauge plastic vinyl sheeting stretched along the long sides, which was supported by chicken wire. Gaps of approximately 15 cm wide were left along the top center line and at the bottom of each long side to allow for hot air dispersal and lateral air flow, respectively, and also allowed some precipitation to fall into the plots. The short sides were also left open to allow further air flow. The shelters were surrounded on both long sides and the short upslope side with 15-cm-deep plastic-lined trenches to reduce lateral soil moisture flow into plots and act as gutters to hold and divert melting snow

shed by the shelter roofs (Fig. 1b). The snowpack reduction treatment resulted in 22% fewer days with snow on the ground during the second winter, with 53 days in the control and 42 under the shelters (methods based on Lundquist and Lott 2008, details in Appendix S1: Fig. S1). We did not measure snowpack during the first winter due to equipment failure. Although the absolute difference in snowpack might have been less in the 2015–2016 winter due to lower overall precipitation, we expect that the relative differences were likely similar since the same proportion of snow was blocked by the shelters. Additionally, although we did not measure snowpack height, we visually observed that the snow reduction treatment also decreased the quantity of snowpack even when some snow passed through the openings in the shelter roofs.

Each treatment was replicated four times ($n = 16$ plots). Because of the sloping design of the snow reduction shelters, snow reduction treatments could not be adjacent on their long sides. Consequently, within each block plots were arranged with the snow reduction treatment applied to two plots adjacent on their short sides, and the shrub removal treatments randomly applied within each pair of reduced snow or ambient snow plots (Fig. 1c).

We planted seeds of two locally dominant native conifer species: *P. ponderosa* and *A. concolor* within all treatment plots. Seeds were provided by the US Forest Service nursery in Placerville, CA, USA. All seeds were collected from California seed zone 526 between 1200 and 1500 m elevation, according to US Forest Service procedure (Buck et al. 1970). We planted 24 seeds of each species in each treatment plot in early October 2015 and again in early October 2016 (24 seeds × 16 plots × 2 species × 2 years = 1536 seeds total). Seeds were planted in a grid pattern within each plot; locations on this grid were randomly assigned to the two species and cohorts. The first cohort of seedlings was not removed prior to the planting of the second cohort.

The King Fire burned in September and October 2014. The shrub removal treatment was established in September 2015, and in both 2015 and 2016, seeds were planted at the beginning of October, with precipitation treatments applied from November to April following planting. In the following warm seasons from April to September, each planted seed was surveyed monthly for emergence and survival. Additionally, we surveyed height to meristem and maximum canopy width of seedlings in September of each year. Seedling height is important for access to light, and canopy width is a proxy for photosynthetic capability and potential surface area for water loss from transpiration.

Year effects

The King Fire burned toward the end of a severe multi-year drought. The planting of the first cohort planting in

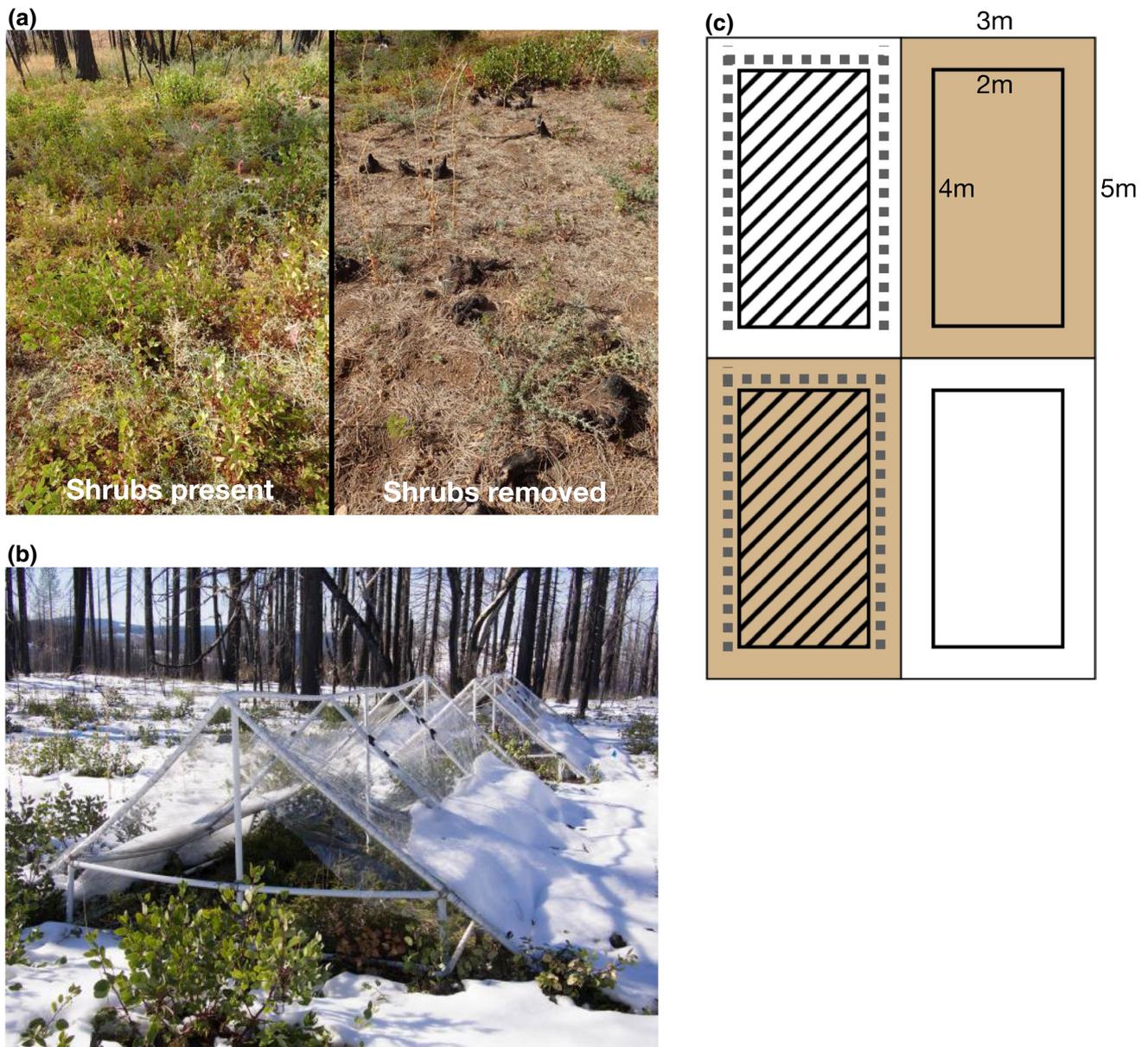


Fig. 1 Photographs and diagram showing details of the experimental design: **a** shrub cover in the shrub present (left) and shrub removal (right) treatment 1 year after treatment established; **b** rain-out shel-

ters. **c** Layout of one block of four plots, showing snow reduction treatment (diagonal lines), trenches (gray dotted lines), herbicide treatment (shaded rectangles). See “[Methods](#)” for details

October 2015 was followed by a fairly average year with 1540 mm of precipitation, but the planting of the second cohort in October 2016 was followed by a historically wet winter, with 2830 mm of precipitation. Winter temperatures following both plantings were similar and somewhat below average (e.g., mean temperature during December and January was 3.6 °C following the first planting and 4.0 °C following the second planting, vs a long-term average of 4.7 °C). In contrast, summer temperatures were significantly higher following the second planting. While

the mean July temperature in 2016 (22.4 °C) was near the 30-year average (22.2 °C), the July temperature in 2017 (23.7 °C) was near the 90th percentile of July temperatures over the 30-year reference period (23.9 °C) (Appendix S1: Fig. S2). We refer in “[Results](#)” and “[Discussion](#)” to the cohort planted in 2015 which experienced relatively average winter and summer conditions in its first year as the “normal cohort”, and the cohort planted in 2016 which experienced a historically wet winter and unusually hot summer as the “extreme cohort.”

Data analysis

All modeling was done in R, version 3.4.3 (R Core Team 2017). To analyze patterns of conifer recruitment, we established mixed-effect models with main effects of snowpack treatment (H1; see “Introduction”), cohort year (H2), shrub presence (H3), and tree species (H4); the two-way interactions between cohort year and snowpack treatment (H2), shrubs and snowpack treatment (H3a), shrubs and cohort year (H3b), tree species and snowpack treatment (H4a), tree species and shrubs (H4b); and a random effect for block. Our response variables of interest were total seedling recruitment, seedling emergence rate and timing, seedling survival duration, and seedling size (height and width). We modeled total seedling recruitment (proportion of seeds planted that emerged and survived to the end of the study) and seedling emergence rate (proportion of seeds planted) on the plot level using generalized linear mixed models with a binomial distribution in the ‘lme4’ package (Bates et al. 2015). Because total recruitment of *A. concolor* was zero in multiple treatments, total seedling recruitment was modeled only for *P. ponderosa*. We modeled emergence timing, height, and width at the seedling level using linear mixed models in the ‘nlme’ package (Pinheiro et al. 2017). Finally, we modeled seedling survival duration using a log-normal distribution and accounting for right censoring (Therneau and Grambsch 2000). We chose to model survival duration in this way to model mortality rates over the 2 years of the experiment. The right censoring approach accounts for a fixed endpoint of the experiment, after which some seedlings were still surviving. This survival analysis was done in the ‘survival’ package in R (Therneau and Grambsch 2000; Therneau 2015). Since the right-censored model approach

does not yet have an option for random effects, block was included as a fixed categorical effect.

We fit models using all possible combinations of the fixed-effect predictors and used model selection based on AICc rankings to select the predictor set that maximized overall model fit, using the ‘MuMIn’ package (Barton 2017). If the best fit model included interaction effects that were not significant (i.e., $p > 0.05$), we reduced the model further to remove the interaction effects. The MuMIn model selection approach did not work with the format of the survival model, so non-significant interactions were removed manually. Coding relied on R packages ‘tidyverse’, ‘plyr’ and ‘lubridate’, and graphs were generated using the R packages ‘ggplot2’, ‘cowplot’, and ‘survminer’ (Wickham 2009, 2011, 2017; Grolemund and Wickham 2011; Kassambara and Kosinski 2018; Wilke 2019).

Results

Total recruitment

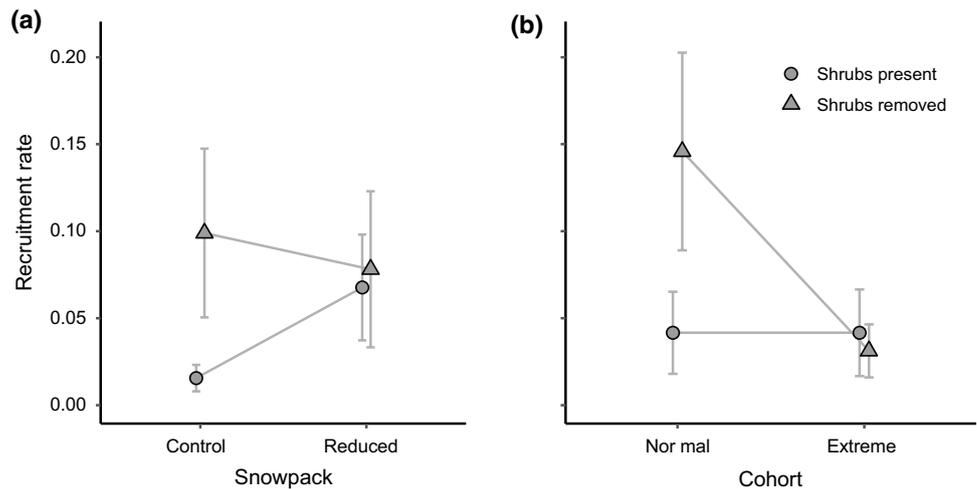
The model for total *P. ponderosa* recruitment included fixed effects for snow reduction, shrub presence, cohort, the interaction between shrub presence and snowpack treatment, and the interaction between shrub presence and cohort (Table 1). *P. ponderosa* recruitment in the reduced snowpack treatment was less negatively affected by shrubs than in the ambient snowpack treatment (Fig. 2a; $z = -2.5$, $p = 0.01$). *P. ponderosa* recruitment of the 2016 cohort (“extreme cohort” planted prior to a historically wet winter and unusually hot summer) was also less negatively affected by shrubs than

Table 1 Selected best models for conifer seedling recruitment, emergence rate, emergence timing, survival duration, and size

Response variable	Intercept	Snow reduction	Shrub removal	Species (PIPO)	Cohort (2016)	Snow × shrub	Cohort × snow	Cohort × shrub
Total recruit rate (PIPO only)	− 5.56 (1.42)	1.58 (0.66)	2.69 (0.71)	−	0.01 (0.53)	− 1.89 (0.77)	−	− 1.82 (0.72)
Emergence rate	− 1.14 (0.19)	− 0.44 (0.20)	− 0.40 (0.16)	0.92 (0.12)	− 0.11 (0.16)	0.49 (0.23)	0.91 (0.12)	−
Emergence timing (months)	3.93 (0.05)	− 0.09 (0.03)	−	0.21 (0.03)	0.29 (0.03)	−	−	−
Survival duration (months)	4.63	0.16	0.29	0.37	− 0.46	−	−	− 0.52
Height (mm)	21.2 (6.31)	10.2 (3.79)	10.1 (3.99)	20.8 (6.26)	− 16.8 (5.10)	−	−	−
Width (mm)	27.0 (4.50)	10.0 (2.69)	8.26 (2.84)	11.3 (4.45)	− 15.9 (3.62)	−	−	−

Fixed effects (with standard errors in parenthesis). “−” Indicates that a parameter was not selected for inclusion in the model (see “Methods”). There were no significant interactions between species and snowpack treatment or species and shrub treatment for any model, so these are not included in the table. Right-censored models of survival duration did not have standard error estimates

Fig. 2 Total recruitment rate per seed of *P. ponderosa* seedlings ± SE by **a** snowpack and **b** cohort, comparing effects of shrub treatment



recruitment of the 2015 cohort (“normal cohort”; Fig. 2b; $z = -2.5, p = 0.01$).

Emergence

Overall, 32% of seeds produced emergent seedlings, with mean emergence of 42% for *P. ponderosa* and 23% for *A. concolor*. The final model of seedling emergence included fixed effects for snow reduction, shrub presence, species, cohort, the interaction between snow reduction and shrub presence, and the interaction between snow reduction and cohort (Table 1). The effect of shrubs was less positive in the reduced snowpack treatment than the ambient snowpack treatment (Fig. 3a; $z = 2.1, p = 0.03$). There was also a significant interaction between snow reduction and seedling cohort (Fig. 3b, $z = 4.0, p < 0.001$). For the normal cohort, emergence was not strongly affected by treatment, but for the extreme cohort, which was planted prior to a historically wet

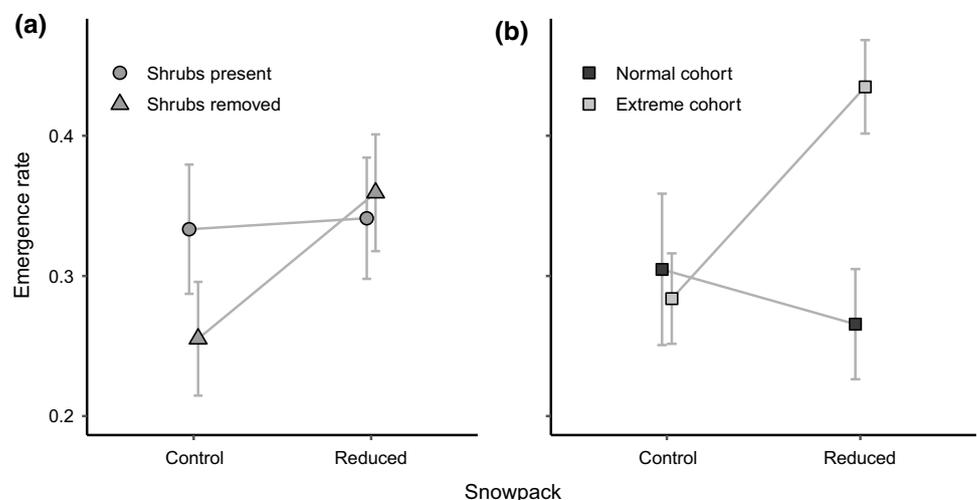
winter, snowpack reduction resulted in an emergence rate 1.5 times that of the unmodified snowpack (43% vs 28%).

The final model of emergence timing included fixed effects for snow reduction, species, and cohort (Table 1). Seedlings in the snow reduction treatment emerged earlier than seedlings in the ambient snowpack treatment ($t = 2.7, p = 0.006$). In addition, seedlings in the normal cohort emerged earlier than those in the extreme cohort ($t = 8.8, p < 0.001$), and seedlings of *A. concolor* emerged earlier than those of *P. ponderosa* (Appendix S1: Fig. S3; $t = 6.08, p < 0.001$).

Survival duration

The final model of survival duration included fixed effects for snow reduction, shrub removal, species, cohort, and the interaction between shrub removal and cohort (Table 1). Snowpack reduction had a positive effect on seedling survival duration (Appendix S1: Fig S4; Wald $\chi^2 = 4.7$,

Fig. 3 Seedling emergence (mean ± SE) in response to snowpack treatment, in **a** response to shrub treatment and **b** for two cohorts. The 2015 cohort was planted prior to a fairly average year, and the 2016 cohort was planted prior to a historically wet winter and a hot summer



$p=0.03$). The effect of shrubs on seedling survival differed by cohort (Wald $\chi^2=12.2$, $p<0.001$), with shrubs having a less negative effect on seedling survival for the extreme cohort than for the normal cohort. Across treatments, survival of *A. concolor* was much lower than that of *P. ponderosa* (Wald $\chi^2=23.1$, $p<0.001$).

Size

The final models for seedling height and seedling width included fixed effects for snow reduction, shrub removal, species, and cohort (Table 1). At the end of the first growing season, seedlings in the snow reduction plots were 10 mm (23%) taller and 10 mm (19%) wider than those in the control snow treatment (height $t=2.7$, $p=0.008$; width $t=3.7$, $p<0.001$). Additionally, seedlings in plots with shrubs were 10 mm (18%) shorter and 8 mm (16%) less wide than

those growing in plots without shrubs (Figs. 4, 5; height $t=2.5$; $p=0.01$; width $t=2.9$, $p=0.005$). In addition to the treatment responses, seedlings in the normal cohort were larger at the end of their first growing season than those in the extreme cohort (height $t=3.3$, $p=0.002$; width $t=4.4$, $p<0.001$). Finally, *P. ponderosa* seedlings were larger than *A. concolor* seedlings (height $t=3.3$, $p=0.001$; width $t=2.5$, $p=0.01$).

Discussion

We provide experimental evidence that post-disturbance weather conditions (both the manipulated snowpack reduction and the natural experiment of seeding in different years) strongly affect the recruitment of dominant tree species in

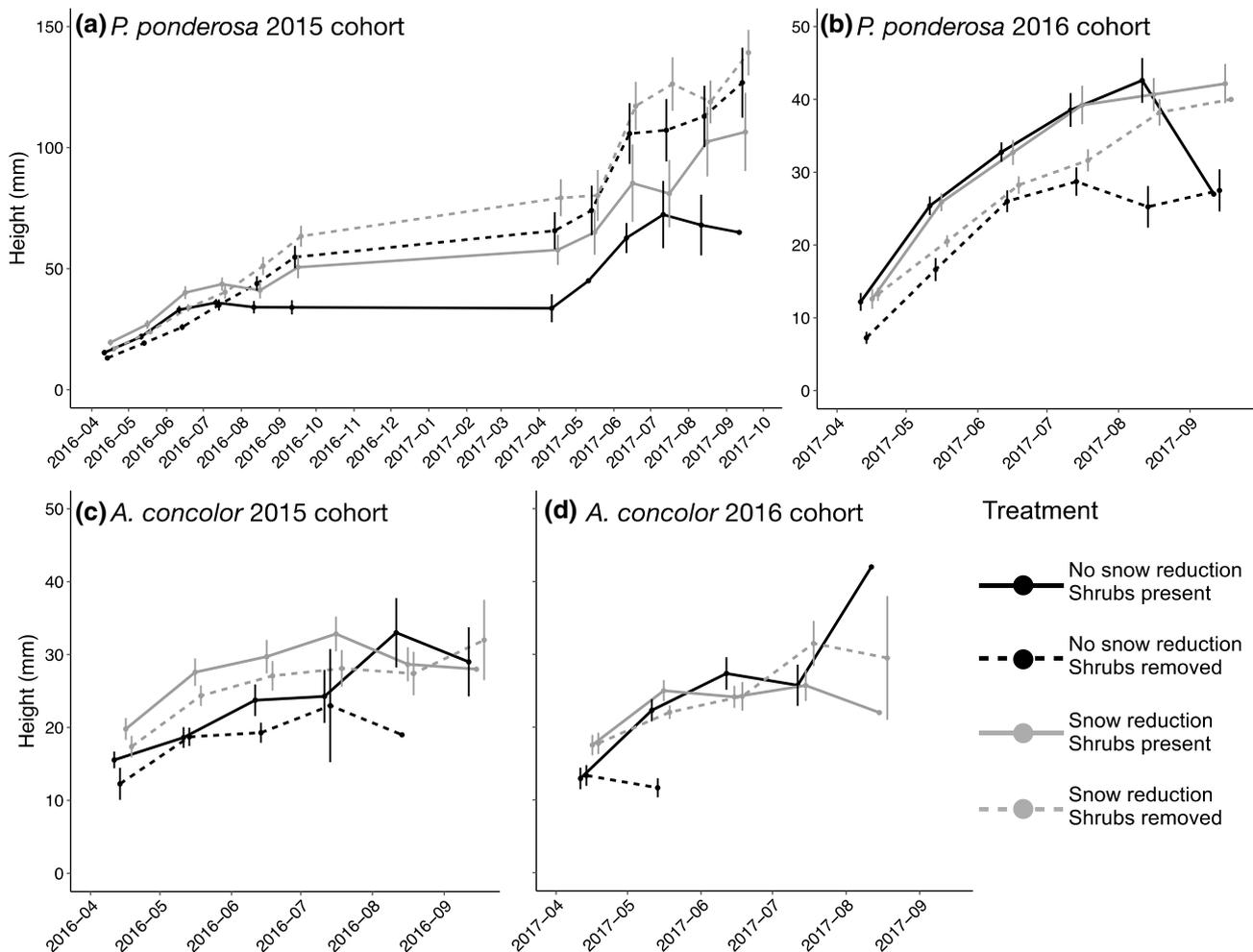


Fig. 4 Height to meristem of seedlings (mean \pm SE) for **a** 2015 cohort of *P. ponderosa* seedlings from April 2016 to September 2017, **b** 2016 cohort of *P. ponderosa* from April 2017 to September 2017, **c** 2015 cohort of *A. concolor* from April 2016 to September 2016 and

d 2016 cohort of *A. concolor* from April 2017 to September 2017. Some lines do not extend for the full time period (for example, all *A. concolor* in the 2016 cohort treatment of no snow reduction, shrubs removed were dead by June 2017)

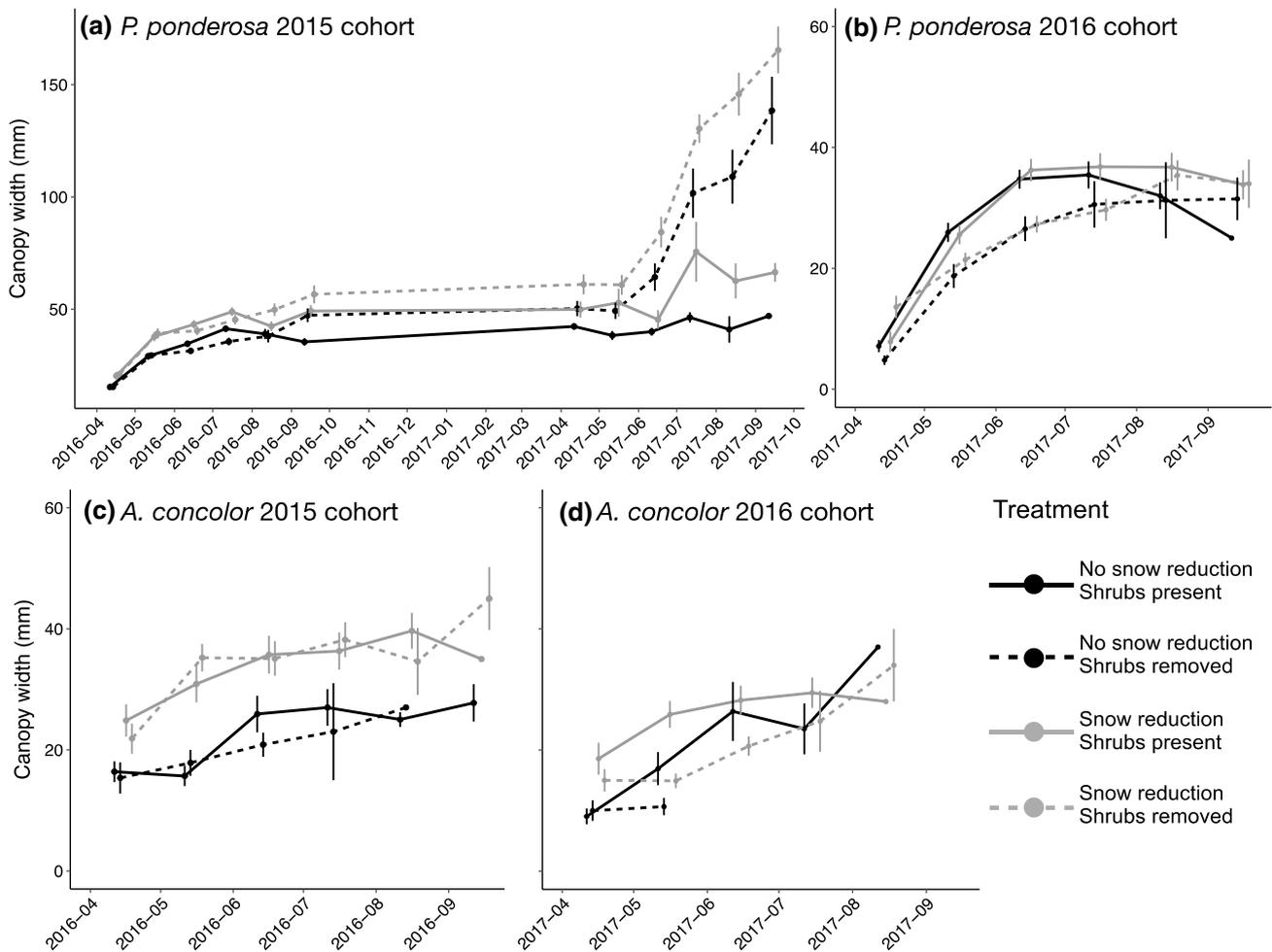


Fig. 5 Canopy width of seedlings (mean \pm SE) for **a** 2015 cohort of *P. ponderosa* seedlings from April 2016 to September 2017, **b** 2016 cohort of *P. ponderosa* from April 2017 to September 2017, **c** 2015 cohort of *A. concolor* from April 2016 to September 2016 and

d 2016 cohort of *A. concolor* from April 2017 to September 2017. Some lines do not extend for the full time period (for example, all *A. concolor* in the 2016 cohort treatment of no snow reduction, shrubs removed were dead by June 2017)

a coniferous forest, and that these effects interacted significantly with experimentally manipulated shrub cover.

H1: Surprisingly positive effects of snow reduction

Contrary to hypothesis 1, reduced snowpack did not decrease emergence, survival, or size of conifer seedlings. Instead, we found that reducing snowpack resulted in earlier emergence timing of seedlings (Appendix S1: Fig. S3), better seedling survival (Appendix S1: Fig. S4), and larger seedlings (Figs. 4, 5). This size difference was likely due to earlier snowmelt allowing for earlier seedling emergence and a consequent head start on the growing season. Although the general expectation for post-fire conifer regeneration has been that of higher recruitment in wetter conditions, a few studies of observed patterns in natural post-fire regeneration have shown evidence of factors

that are associated with earlier snowmelt—e.g., warmer springs (Little et al. 1994) and more growing degree days (Urza and Sibold 2017)—increasing recruitment and/or affecting establishment timing of some species but not others. Both of these studies took place in subalpine systems, which are generally expected to be more limited by growing season length than mid-elevation mixed-conifer forest. Additional studies in unburned systems have also documented negative effects of snow duration on conifer seedling survival and growth (Ettinger and HilleRisLambers 2017). Our results also add experimental evidence to the observations that the impact of overall precipitation on post-fire regeneration depends on seasonal timing in both subalpine systems and the hot and dry portion of *P. ponderosa*'s range (Feddema et al. 2013; Urza and Sibold 2017).

H2: Temporal variation in recruitment conditions

One cohort experienced a fairly average first year, with relatively average winter precipitation as well as summer precipitation and temperatures, while the other experienced historically high winter precipitation and snow, and then a particularly dry and hot summer (Appendix S1: Fig. S2). Consistent with hypothesis 2, these planting years had strong effects on the patterns observed, including total recruitment (Fig. 2). For the extreme cohort (but not the normal one), seedlings in the snowpack reduction treatment had higher emergence as well as earlier emergence timing (Fig. 3b; Appendix S1: Fig S3), indicating that abnormally high levels of winter precipitation (as experienced by the extreme cohort trees not receiving snowpack reduction treatment) can also have negative effects on post-fire regeneration. The survival of the extreme cohort through the hot and dry summer was much lower than that of the normal cohort, which was in their second growing season at that point (Appendix S1: Fig S4). These differences demonstrate the importance of establishment year in determining regeneration outcomes.

Studies across dry mixed-conifer forest, moist mixed-conifer forest, and subalpine forest have recently observed patterns of lower recruitment in warm and dry years (Harvey et al. 2016; Stevens-Rumann et al. 2018; Young et al. 2018). These results of differences between cohorts, combined with our snow reduction experiments, suggest that those observations are more likely to be driven by hotter summers, which increase both heat stress and drought stress on seedlings, than by decreases in snow load. It has been proposed that contrasting effects of climate change on different life stages (“demographic compensation”) may influence species’ net responses to changing climate (Doak and Morris 2010). We found contrasting seasonal effects on different seedling life stages (Table 1). In a warmer climate, the positive effects of reduced snowpack on conifer emergence and size may somewhat buffer the negative effects of hot summers on survival and size. These contrasting results are consistent with a limiting factors framework: at the start of the growing season, seedling emergence and growth is mostly likely warmth-limited, in which case the snowpack reduction treatment had positive effects (Fig. 3). But later in the growing season, water becomes more limiting, as well as potential damage from too-high temperatures, so the hot summer had negative effects (Figs. 4, 5). Even under less favorable future climates, cooler or wetter summers coinciding with regeneration stages may allow recruitment on the landscape if seedlings can establish successfully (Serra-Diaz et al. 2015).

H3: Interacting effects of competition and climate can facilitate or impede recruitment

Our study indicates that shrub–seedling interactions may vary with weather conditions, with the cumulative balance of these effects shifting under different abiotic conditions in different years. For example, shrubs decreased *P. ponderosa* recruitment in the control snowpack treatment, but had essentially no effect in the reduced snowpack treatment (Fig. 2). Although this finding was consistent with hypothesis 3a, that biotic interactions with shrubs would be less negative in the snowpack reduction treatment, we could not connect the result to more stressful abiotic conditions (Bertness and Callaway 1994), as the snowpack reduction treatment did not have an overall negative effect on conifer seedlings. The net neutral effect of shrubs on seedling survival in the snowpack reduction treatment could either have been due to the snow removal treatment weakening the negative effects of competition with shrubs if the longer growing season gave seedlings more successful access to limiting resources (including soil moisture and light), or due to an increase of the positive effects of shrubs if the seedlings benefitted more strongly from shrub facilitation under reduced snowpack conditions. The difference between snowpack treatments in shrub–conifer interactions may have been caused by the priority advantages of resprouting or early germinating shrubs being reduced when conifers were able to germinate earlier (due to a reduction in snowpack and thus earlier snow melt). However, the interaction between shrubs and snowpack treatment was consistent across cohorts (despite large differences in weather between years), even though shrubs would have had over a year of establishment before the extreme cohort was planted, so any difference in priority is likely to be driven by seasonal advantages in the early growing season.

Consistent with hypothesis 3b, the effects of shrubs were less negative (and potentially facilitative) for the cohort that had lower overall recruitment, the extreme cohort. This difference was most strongly observed in the survival duration of seedlings (Appendix 1: Fig. S4). Survival through the first growing season may have been dependent on stressors of water limitation, extreme heat, herbivory, and/or light limitation. If water limitation were the main stressor, we would have predicted that shrubs would still be competitive rather than facilitative (Maestre et al. 2009). However, it is possible that the facilitative benefits of decreased transpiration or evapotranspiration outweighed competition for soil moisture, as has been observed with “nurse shrub” phenomena in some arid systems (Kitzberger et al. 2000; Gómez-Aparicio et al. 2004; Stultz et al. 2007; Holmgren et al. 2011). Additionally, shading by shrubs can decrease temperature, another potential stressor that would be exacerbated in a hot summer.

Primary stressors or limiting factors may also vary by life stage. In contrast with survival, we observed consistently negative effects of shrubs on size (Figs. 4, 5), possibly because growth is more strongly limited by light, for which shrubs would be purely competitive. In a warming climate, these contrasting effects of shrubs on different life stages may cancel out in some circumstances (Doak and Morris 2010).

H4: Species responded similar to treatments

In contrast with hypothesis 4, the two tree species did not differ in their responses to the snow reduction or the shrub removal treatments. However, overall emergence and survival of *A. concolor* seedlings were lower than that of *P. ponderosa* seedlings. This could have been driven by the viability of the seed sources themselves rather than generalizable differences; however, it is also possible that the severely burned setting with no canopy cover and direct light was harsher for the shade-tolerant *A. concolor* than *P. ponderosa* even underneath shrub cover (Barker 2011). *Abies concolor* seedlings also emerged earlier than *P. ponderosa* seedlings, possibly due to being more adapted to higher elevation and mesic environments (Safford and Stevens 2017) or responses to different environmental cues.

Implications for management

Especially as climate change leads to longer and more extreme fire seasons and increasing area burned at high-severity, long-term forest structure and composition are likely to depend on recruitment of regenerating species. High-severity fires can leave burned regions bare of adult conifers and far from seed trees, in which natural regeneration may be low or even absent (Welch et al. 2016). However, even in burned areas where seed sources are present, abiotic and biotic conditions may result in low germination or survival rates, and consequently insufficient regeneration. Our results indicate that warm winters may have positive effects on regeneration, while warm summers are likely to have negative effects. Managers can partially compensate for this variation in natural regeneration by planting more seedlings following hot, dry years. In the future, it may be advisable to include flexibility that permits planting schemes to be shifted from warm to cool slopes or vice versa as the nature of the planting season becomes apparent. Additionally, because shrub cover can have neutral or even positive effects on conifer survival in years with lower snowpack and/or hot summers, it may be beneficial to retain some moderate level of shrub cover in burned landscapes, so as to take advantage of the facilitative benefits of shading to seedling survival in the dry season. In the same vein, planting can also take advantage of remnant tree cover on burned site

(Dobrowski et al. 2015). On the other hand, if rapid growth of planted conifers is the management focus, some level of shrub control will probably be advisable, as our work shows that conifer growth is lower in plots with shrubs regardless of weather conditions. Although complex interactions present a challenge to modeling and decision-making for conservation and management, research into interacting factors ultimately improves our insight into the complex ecological patterns that shape natural systems and increases our ability to predict and adapt to the effects of future climatic conditions on these systems.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Data and code Data and R code are available in a figshare repository, <https://doi.org/10.6084/m9.figshare.3172468>.

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