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# Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest

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## Abstract

Climate niche models project that subalpine forest ranges will extend upslope with climate warming. These projections assume that the climate suitable for adult trees will be adequate for forest regeneration, ignoring climate requirements for seedling recruitment, a potential demographic bottleneck. Moreover, local genetic adaptation is expected to facilitate range expansion, with tree populations at the upper forest edge providing the seed best adapted to the alpine. Here, we test these expectations using a novel combination of common gardens, seeded with two widely distributed subalpine conifers, and climate manipulations replicated at three elevations. Infrared heaters raised temperatures in heated plots, but raised temperatures more in the forest than at or above treeline because strong winds at high elevation reduced heating efficiency. Watering increased season-average soil moisture similarly across sites. Contrary to expectations, warming reduced Engelmann spruce recruitment at and above treeline, as well as in the forest. Warming reduced limber pine first-year recruitment in the forest, but had no net effect on fourth-year recruitment at any site. Watering during the snow-free season alleviated some negative effects of warming, indicating that warming exacerbated water limitations. Contrary to expectations of local adaptation, low-elevation seeds of both species initially recruited more strongly than high-elevation seeds across the elevation gradient, although the low-provenance advantage diminished by the fourth year for Engelmann spruce, likely due to small sample sizes. High- and low-elevation provenances responded similarly to warming across sites for Engelmann spruce, but differently for limber pine. In the context of increasing tree mortality, lower recruitment at all elevations with warming, combined with lower quality, high-provenance seed being most available for colonizing the alpine, portends range contraction for Engelmann spruce. The lower sensitivity of limber pine to warming indicates a potential for this species to become more important in subalpine forest communities in the coming centuries.

**Keywords:** alpine treeline, climate change experiment, Engelmann spruce, limber pine, *Picea engelmannii*, *Pinus flexilis*, seedling demography, species range shift

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## Introduction

Shifts in the geographic distributions of species are a widely anticipated consequence of global warming (Chen *et al.*, 2011; Moritz & Agudo, 2013), especially in high-elevation ecosystems where temperature is thought to be a primary constraint (Lenoir *et al.*, 2008; Gottfried *et al.*, 2012; Pauli *et al.*, 2012). In particular, projections using climate niche models suggest rapid upslope shifts in habitat suitable for subalpine trees with warming (e.g., Rehfeldt *et al.*, 2006; Monahan

*et al.*, 2013). Low summer temperatures have been observed to limit tree growth above treeline (Rossi *et al.*, 2008; Korner, 2012) and 20th c. warming led to increased tree growth and migration to higher elevations, especially where the magnitude of warming was large (Harsch *et al.*, 2009; Salzer *et al.*, 2009). However, evidence from high-latitude Siberian forests (Frost & Epstein, 2014) to low-latitude cloud forests (Rehm & Feeley, 2015) indicates that moisture can also limit upper treeline position. For example, while Holocene warming generally resulted in tree advances upslope in the western United States (Morgan *et al.*, 2014) and Europe (Schwoerer *et al.*, 2014), fluctuations in temperature, moisture, or both drove regionally synchronous

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retreats in treeline elevations (Morgan *et al.*, 2014). At lower elevations, increased exposure to acute and chronic water stress is increasing tree mortality in woodlands and forests (Van Mantgem *et al.*, 2009), including subalpine forests (Smith *et al.*, 2015), although persistent global change effects can be difficult to distinguish from natural modes of variability (Fellows & Goulden, 2012). However, recent studies have also suggested that, with climate change, some populations may shift down slope (Lenoir *et al.*, 2010) due to increased precipitation (Crimmins *et al.*, 2011; but see Stephenson & Das, 2011), net cooling effects from cold-air drainage (Van de Ven *et al.*, 2007), or altered interactions with other species. Thus, upper and lower tree distribution limits can be dynamically sensitive to both temperature and moisture.

Tree recruitment above treeline is required for upward forest range expansion. Similarly, lack of recruitment at the low-elevation edge of a species' range ultimately leads to range contraction. Seedling germination and establishment are particularly climate sensitive (Walck *et al.*, 2011) and could determine whether and how fast elevation shifts occur (Malanson *et al.*, 2007; Smith *et al.*, 2009). Observational studies that relate periods of tree establishment to particular climatic regimes or compare climate envelopes of adults and juveniles have provided valuable insights (Ibanez *et al.*, 2007; Lenoir *et al.*, 2009; Mclaughlin & Zavaleta, 2012; Zhu *et al.*, 2012; Dobrowski *et al.*, 2015; Millar *et al.*, 2015), but cannot distinguish climate effects on establishment from seed availability or reliably disentangle temperature and moisture effects. To project range shifts with climate change, models require distinguishing among these varied climate and demographic influences on recruitment. Experimental investigations of climate controls on subalpine seedling recruitment have found greater survival and recruitment with greater precipitation or soil moisture, including at and above treeline, albeit with species differences in sensitivity (Gill *et al.*, 2015; Tingstad *et al.*, 2015; Loranger *et al.*, 2016). Experimentally determined effects of temperature on subalpine tree recruitment are somewhat more idiosyncratic, depending on landscape position, neighboring vegetation, and life stage (Grau *et al.*, 2013; Zurbriggen *et al.*, 2013; Loranger *et al.*, 2016). Warming more consistently enhances growth of established seedlings at high elevations (Danby & Hik, 2007; Grau *et al.*, 2013; Zurbriggen *et al.*, 2013). However, most *in situ* temperature manipulation studies use open-top chambers, which introduce reinforcing and countervailing effects. They reduce wind speed and can decrease nighttime temperatures among other effects, which also alter seedling performance.

Finally, local adaptation to historical climate may leave seedlings poorly adapted to the new climate,

requiring dispersal to new, upslope locations to maintain fitness (Rehfeldt *et al.*, 1999; Wang *et al.*, 2010; Valadares *et al.*, 2014). Genetic differentiation has been found across vertical (elevation) distances of just 200–450 m for Rocky Mountain conifers (reviewed in Mitton, 1995). Alternately, gene flow among populations, which is thought to be high for wind-pollinated trees, and phenotypic plasticity may enable populations to track the changing climate and maintain fitness, facilitating both persistence and range shifts (Kremer *et al.*, 2012; Alberto *et al.*, 2013). Quantifying the climatic and genotypic factors affecting recruitment is critical to understanding and projecting how climate change will alter forest distribution and composition.

Here, we report the effects of experimental climate change on seedling recruitment for two subalpine conifers widely distributed in North America, limber pine (*Pinus flexilis* James) and Engelmann spruce (*Picea engelmannii* Parry ex. Engelm), at three elevations at Niwot Ridge, Colorado, USA. We used infrared heating and watering during the growing season to separate temperature and moisture effects. Across 5 years, we sowed >750 000 seeds collected locally from high- and low-elevation provenances to assess the importance of genetic variation. Our experiment was designed to answer the following questions: (i) How does warming alter initial tree recruitment and recruitment to 4 years across and beyond the elevation range of subalpine forest? (ii) What effects does supplemental summer water have on recruitment at low and high elevations? (iii) How does seed source affect recruitment and responses to climate treatments? (iv) How do these responses differ between late-seral Engelmann spruce and shade-intolerant limber pine? Our prior work has shown that warming can increase moisture stress in establishing limber pine, reducing photosynthesis and respiration, as well as initial seedling survival (Moyes *et al.*, 2013). At treeline, and with warming in the alpine, temperature and moisture appear to colimit seasonally integrated seedling carbon assimilation (Moyes *et al.*, 2015). We have also found provenance differences in germination and early seedling survival (Castanha *et al.*, 2013), as well as in metabolic rates and seedling size (Reinhardt *et al.*, 2011). This analysis extends our prior work, evaluating the importance of early physiological and demographic responses to later outcomes over a wider range of experimental and interannual climate variability.

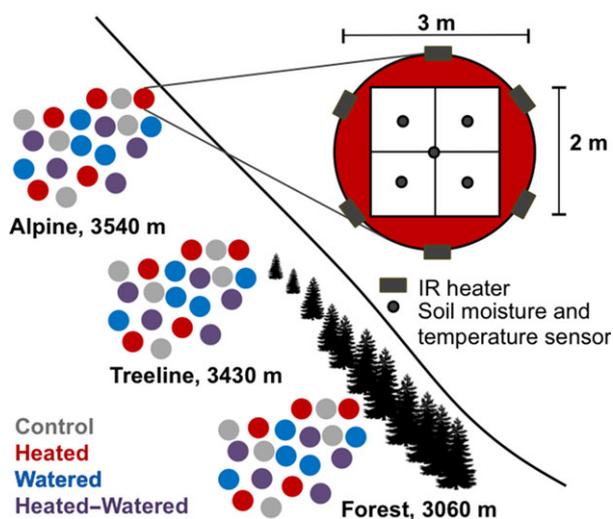
## Materials and methods

### Experimental design

Our study was conducted at Niwot Ridge, on the eastern slope of the Rocky Mountains in Colorado, USA. We established

experimental sites in (i) a stand of mature trees near the low-elevation edge of subalpine forest (3060 m), (ii) an open meadow surrounded by krummholz mats and low tree islands at upper treeline (3430 m), and (iii) an alpine meadow approximately 400 m upslope from local timberline (3540 m; Fig. 1, Table 1). Soils were thin and rocky at all sites, with higher organic matter in the treeline and alpine sites than in the forest, and a ~2-cm organic horizon in the forest site (Castanha *et al.*, 2013). During the period of the experiment, ambient annual air temperature differed by 4.6 °C across the three experimental sites and mean snow-free season length differed by 30 days (Table 1). Snowfall is typically greater at higher elevations at Niwot Ridge due to orographic effects (Kittel *et al.*, 2015), but snow depth is locally variable due to substantial wind redistribution, and was greatest at the treeline site. Aside from an extreme rainfall event in September 2013, which resulted in significant flooding at lower elevations and raised plot soil moisture but did not damage or otherwise directly affect our research sites, climate variability during the years of the experiment (2009–2014) was within the range of historical climate variability documented by the nearest USHCN station in Boulder, CO, from 1931 to 2014.

Each site had 20 circular, 3-m-diameter plots assigned to four groups: control, heated, watered, and heated and watered (Fig. 1). Six 1000-W infrared heaters arrayed around the perimeters of heated plots (following the geometry of Kimball *et al.*, 2008) with constant heater output (following Harte *et al.*, 1995) raised mean daily 5–10 cm soil temperature (ECTM and



**Fig. 1** Experimental design for the Alpine Treeline Warming Experiment. Sixty plots were sown annually with high- and low-elevation limber pine and Engelmann spruce seeds in separate quadrants. The alpine site is above treeline, the treeline site is at the upper elevation edge of subalpine forest, and the forest site is near the low-elevation edge of subalpine forest. Soil temperature and moisture sensors recorded microclimate at the center of the four quadrants. Six infrared heaters were suspended at 1.2 m on scaffolding that could be lifted and lowered with the accumulation and melt of snow. Watered plots received 2.5 mm water per week during the growing season.

5TM sensors; Decagon Devices, Pullman, WA, USA) during the snow-free periods, with larger increases (+3.8 °C) in the forest than in the alpine and treeline (+1.4 and +1.7 °C, respectively) sites because greater wind speed at high elevations reduced heating efficiency (Kimball *et al.*, 2008) (Table 1). Seedlings are tightly coupled to near-surface air temperature, which is well predicted from soil temperature (Moyes *et al.*, 2015). Our model for air temperature at 1 cm during the 2012 snow-free season indicates that our heating treatments increased near-surface air and seedling temperatures by only 0.2 °C (alpine), 0.1 °C (treeline), and 0.6 °C (forest) more than they increased soil temperatures. Except in 2009–2010, heater output was reduced between November and March, the windiest time of year, to avoid hydrological artifacts and potentially intermittent snowpack (Meromy *et al.*, 2015). Heating also extended the snow-free season and reduced summer soil moisture (Table 1). We designed the watering treatments (2.5 mm week<sup>-1</sup>) to compensate for evaporative losses due to heating, adding water manually with hand-held sprayers once per week, starting 2–3 weeks after snow melt and ending in September. Watering slightly increased soil volumetric water content (+0.01 m<sup>3</sup> m<sup>-3</sup>) at 5–10 cm depth at all sites (Table 1).

### Seedling recruitment

Our two focal species are widely distributed in Western North America. Engelmann spruce (*P. engelmannii* Parry ex. Engelm.) occurs at high elevations up to treeline in the Rocky Mountains and in the Cascade Ranges. Limber pine (*P. flexilis* James) also occurs up to treeline in the Rocky Mountains, Sierra Nevada, and Great Basin ranges. Unlike the late-seral, shade-tolerant Engelmann spruce, limber pine is often a shade-intolerant pioneer species and can persist on exposed, infertile sites. Both species can live for hundreds or >1000 years. Each autumn, we collected local seeds from high (3370–3570 m) and low (2910–3240 m) elevations (Castanha *et al.*, 2013). Each species and seed provenance was randomly assigned to one of four 1 × 1 m quadrats nested within each 7.1-m<sup>2</sup> circular plot at the start of the experiment. We sowed 280–1400 seeds per quadrat each autumn (>750 000 seeds total over 5 years), depending on seed viability (as determined by X-ray analysis) and availability. For each provenance and year, we collected 200–1300 limber pine cones from trees and 1500 to 15 000 Engelmann spruce cones from new caches (we estimate an average of 15–70 cones per tree, with some inter-annual variability). When new seed availability was low, we sowed excess seed from a prior year that had been stored at –20 °C. USFS personnel extracted Engelmann spruce seed from cones and dewinged it in their Coeur d’Alene nursery, and we extracted limber pine seed from cones. Seed was not treated prior to sowing and was carefully blended among source trees to ensure comparable seed went into all plots. Initial trials transplanting glasshouse-started seedlings into the experimental plots were discontinued after we determined that survival rates were elevated for transplants relative to *in situ* germinants (Castanha *et al.*, 2013). To exclude small mammals, we placed hardware cloth cages (1-cm<sup>2</sup> openings) over each plot. The enclosures substantially reduced granivory and herbivory (Castanha *et al.*, 2013); remaining noise in the

**Table 1** Field site climate and treatment effects on microclimate

	Elev. (m)	Mean air T (°C)	PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Wind ( $\text{m s}^{-1}$ )	SL (days)	$\Delta T_{\text{H}}$ (°C)	$\Delta \text{SL}_{\text{H}}$ (days)	$\Delta \text{VWC}_{\text{H}}$ ( $\text{m}^3 \text{m}^{-3}$ )	$\Delta \text{VWC}_{\text{W}}$ ( $\text{m}^3 \text{m}^{-3}$ )
Forest	3060	9.8 (0.4)	179 (9)	0.2 (0.0)	158 (9)	3.81 (0.04)	38 (10)	-0.012 (0.001)	0.014 (0.0004)
Treeline	3430	7.4 (0.5)	448 (13)	3.6 (0.2)	133 (6)	1.72 (0.05)	12 (4)	-0.012 (0.001)	0.008 (0.001)
Alpine	3540	6.7 (0.5)	446 (12)	5.8 (0.3)	140 (11)	1.38 (0.03)	10 (2)	-0.016 (0.001)	0.008 (0.001)

Daily mean (2010–2014) site climate and treatment effects during the snow-free season, with standard errors in parentheses. Abbreviations are photosynthetically active radiation (PAR); snow-free season length (SL; determined from diel variability in soil temperature in unheated plots); heating effects on 5–10 cm soil temperature ( $\Delta T_{\text{H}}$ ), snow-free season length ( $\Delta \text{SL}_{\text{H}}$ ), and 5–10 cm soil volumetric water content ( $\Delta \text{VWC}_{\text{H}}$ ); and watering effect on 5–10 cm soil volumetric water content ( $\Delta \text{VWC}_{\text{W}}$ ).

data from damage by animals was likely greatest at the forest site where small mammal pressure was greatest (C. Castanha, personal observation). We tracked the number of seeds sown and number of seedlings surviving to autumn of each year for each cohort. The 2010 and 2011 cohorts were observed for 4 years, the 2012 for 3 years, the 2013 for 2 years and the 2014 for 1 year.

### Statistical analysis

Due to the differences in heating effects on soil and plant temperatures across sites, we estimated effects of heating, watering, provenance and all two-way interactions on seedling recruitment and survival separately for each site using generalized linear mixed effects models (function `lme4::glmer` in R 3.1.2 package `mgcv`) with a logit link and binomial distribution. We present summary results in figures and tables below, with full results of statistical analyses, including parameter estimates, for first-year and fourth-year recruitment, as well as year-to-year survival of Engelmann spruce and limber pine seedlings in the following tables: first-year recruitment (Tables S1 and S2), fourth-year recruitment (Tables S3 and S4), first- to second-year survival (Tables S5 and S6), second- to third-year survival (Tables S7 and S8), and third- to fourth-year survival (Tables S9 and S10). For models of first-year recruitment, random effects included cohort year, plot within cohort year, and an observation-level random effect to accommodate overdispersion. For models of fourth-year recruitment and year-to-year survival, cohort year was instead treated as a fixed effect.

Prior to running the statistical models and hypothesis tests, we performed exploratory analyses on first-year recruitment to determine how many interactions to include in hypothesis testing. We used `MuMIn::dredge` to compare all possible models (Burnham & Anderson, 2002). Using a model formulation that includes greater than second-order interactions with a limited data set would have so many terms that no effects would be estimated well. More years of data or more replicates would be necessary to determine full interactions among the four crossed factors employed in our experiment.

Significance levels were estimated using likelihood ratio tests. Using a hypothesis-testing framework, which is consistent with a manipulation experiment, we determined which estimated effects, inclusive of all possible two-way interactions, are not consistent with chance under null hypotheses.

Because GLMM likelihood ratio tests in R do not automatically compute a likelihood ratio for main effects separately from their interactions, to test main effects we directly manipulated the design matrix (`stats::model.matrix`). In manipulating the design matrix, we chose effect, or deviation, coding (using `'contr.sum'` in R). Thus, the intercepts for the models represent the average recruitment (or survival) across all factors. The coefficient estimates in the Tables S1–S11 represent the deviation from this average for a given treatment. Thus, all levels across a factor should sum to zero (where there are two levels, we present just one since the other is the same magnitude but opposite sign). We mention this because this is not the default output in `lme4::glmer`.

As a measure of the amount of variation explained by each model, we computed both marginal and conditional  $R^2$  values following the method of Nakagawa & Schielzeth (2013) using `MuMIn::r.squaredGLMM` (Table S11). Marginal  $R^2$  reflects variance explained only by fixed factors, whereas conditional  $R^2$  reflects variance explained by fixed and random factors in each model.

## Results

### Heating effects

Consistent with the hypothesis that warming near the low-elevation edge of subalpine forest would reduce recruitment, we found dramatic decreases in first-year recruitment (survival to end of the first growing season as fraction of sown seeds) (Tables 2, 3, S1 and S2), by 95% and 62% for Engelmann spruce and limber pine, respectively (Fig. 2a, b). Contrary to our expectations that warming at high elevations would increase recruitment, we found, instead, that warming reduced first-year recruitment at treeline (-28.3% and -22.6% for Engelmann spruce and limber pine) and alpine (-16.0% and -11.7%) sites, although these effects were marginal ( $0.05 < P < 0.11$ ) for limber pine (Fig. 2a, b; Tables 2, 3, S1 and S2).

As seedlings matured, we detected less sensitivity to warming for Engelmann spruce (Tables S3, S5, S7, S9), possibly as a result of reduced sample sizes, culling of more frail individuals, or because of physiological or

**Table 2** Generalized linear mixed effects model likelihood ratio tests (LRT) and  $P$ -values,  $P(\chi^2)$ , for main effects and all two-way interactions on first-year recruitment of Engelmann spruce

Engelmann spruce Seed to first year	Forest		Treeline		Alpine	
	LRT (df)	$P(\chi^2)$	LRT (df)	$P(\chi^2)$	LRT (df)	$P(\chi^2)$
Heat	46.26 (1)	<b>&lt;10<sup>-5</sup></b>	11.54 (1)	<b>0.00068</b>	4.02 (1)	<b>0.045</b>
Water	4.80 (1)	<b>0.028</b>	10.34 (1)	<b>0.0013</b>	10.80 (1)	<b>0.0010</b>
Provenance	6.06 (1)	<b>0.014</b>	6.22 (1)	<b>0.013</b>	24.89 (1)	<b>&lt;10<sup>-5</sup></b>
Heat × water	2.76 (1)	0.097	0.03 (1)	0.85	0.024 (1)	0.88
Heat × provenance	0.81 (1)	0.37	1.07 (1)	0.30	0.14 (1)	0.70
Water × provenance	0.36 (1)	0.55	0.02 (1)	0.90	0.03 (1)	0.87

Random effects variances (for forest, treeline, and alpine, respectively) are 1.08, 1.82, and 4.14 for cohort year, 3.92, 0.64, and 0.55 for plot (nested in cohort year), and 2.13, 0.46, and 0.42 for the observation-level random effect.  $P < 0.05$  are given in bold type. All parameter estimates are given in Table S1.

**Table 3** Generalized linear mixed effects model likelihood ratio tests (LRT) and  $P$ -values,  $P(\chi^2)$ , for main effects and all two-way interactions on first-year recruitment of limber pine

Limber pine Seed to first year	Forest		Treeline		Alpine	
	LRT (df)	$P(\chi^2)$	LRT (df)	$P(\chi^2)$	LRT (df)	$P(\chi^2)$
Heat	31.91 (1)	<b>&lt;10<sup>-5</sup></b>	2.60 (1)	0.11	3.72 (1)	0.054
Water	1.38 (1)	0.24	0.05 (1)	0.82	2.42 (1)	0.12
Provenance	17.84 (1)	<b>2.4 × 10<sup>-5</sup></b>	62.29 (1)	<b>&lt;10<sup>-5</sup></b>	64.12 (1)	<b>&lt;10<sup>-5</sup></b>
Heat × water	0.03 (1)	0.85	0.19 (1)	0.66	0.55 (1)	0.46
Heat × provenance	0.42 (1)	0.52	0.01 (1)	0.91	0.68 (1)	0.41
Water × provenance	0.08 (1)	0.78	0.09 (1)	0.77	0.04 (1)	0.84

Random effects variances (for forest, treeline, and alpine, respectively) are 1.25, 1.37, and 1.31 for cohort year, 1.00, 0.44, and 0.11 for plot (nested in cohort year), and 1.16, 0.60, and 0.86 for the observation-level random effect.  $P < 0.05$  are given in bold type. All parameter estimates are given in Table S2.

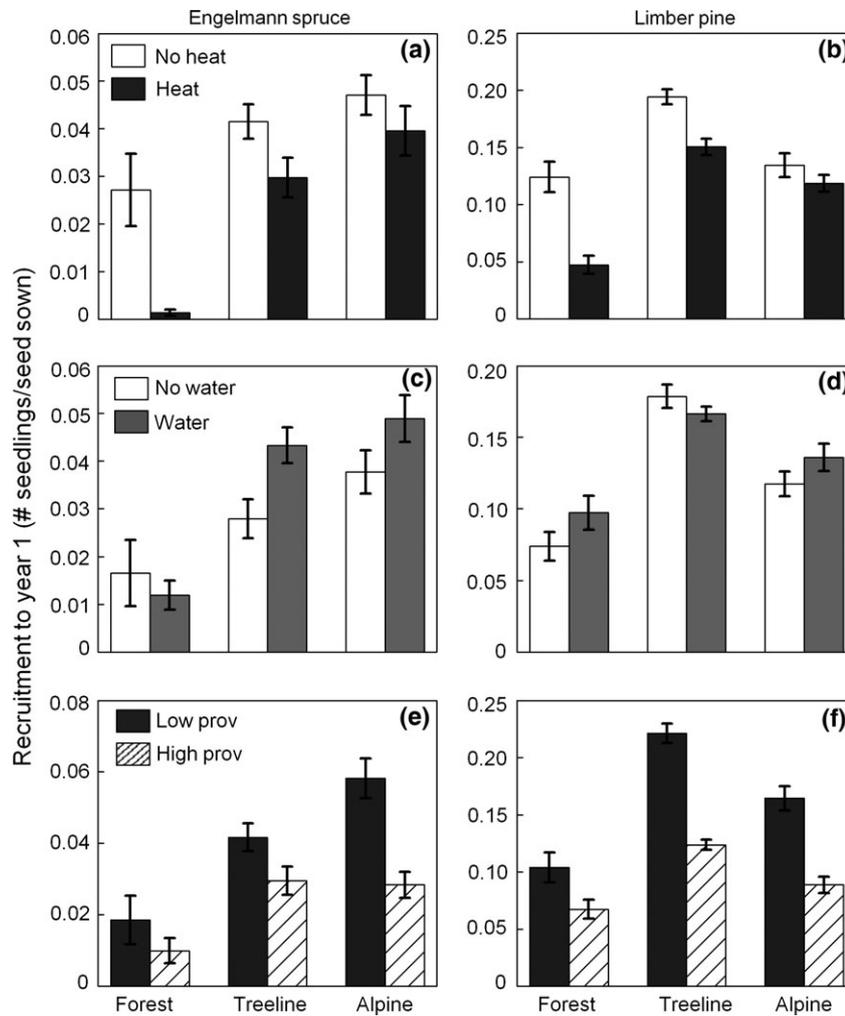
morphological changes. Specifically, first- to second-, second- to third-, and third- to fourth-year Engelmann spruce survival were not significantly affected by warming at any site ( $P > 0.06$ ). Therefore, the negative effect of warming in the first year carried through to the fourth year at treeline and alpine sites (Table 4, Fig. 3). Heating effects were more pronounced in the 2010 cohort than the 2011 cohort at treeline and in the alpine, although this interaction was marginally significant in the alpine (Tables 4 and S3). At the forest site, no Engelmann spruce seedlings survived to their fourth year in heated plots (lines that stop before year four in Fig. 3e, f), emphasizing the early and acute sensitivity of this species to warming at low elevation. In treeline and alpine sites, 9.3% and 41.3% fewer seedlings survived to their fourth year in heated and unheated plots, respectively (Tables 4 and S3).

Seedling survival actually increased with warming for limber pine seedlings at forest and alpine sites in the second to third year ( $P < 0.05$ ; Table S8), with a significant heat by cohort year interaction at the treeline site ( $P = 0.0072$ ). Ultimately, for limber pine, there was

no net effect of warming on recruitment to the fourth year; the later benefits of warming reversed, but did not overcome, the negative effect of warming on first-year recruitment in any site (Tables 5 and S4; Fig. 4).

#### Watering effects

Consistent with our hypothesis that additional summer moisture would enhance recruitment, first-year recruitment increased with watering across sites for Engelmann spruce (Fig. 2c; Tables 2 and S1), but was not significantly different for limber pine at any site (Fig. 2d; Tables 3 and S2). For Engelmann spruce, benefits of watering diminished through time, with effects on year-to-year seedling survival and fourth-year recruitment marginal or not significant ( $P > 0.06$ ; Tables S3, S5, S7, S9), likely due in part to declining sample sizes. For limber pine, watering increased first- to second-year survival at all sites ( $P < 0.05$ ; Table S6), and ultimately increased recruitment to the fourth year at the forest site (Fig. 4), where heating significantly diminished the benefits of watering (Tables 5 and S4).



**Fig. 2** First-year recruitment. Mean seedling recruitment (as fraction of sown seed) to the end of the first growing season by site for Engelmann spruce (a, c, e) and limber pine (b, d, f) as affected by heating (a, b), watering (c, d), and seed provenance (e, f) calculated from plot-level averages of the raw data across years to avoid pseudoreplication. Treatment and provenance group error bars (one standard error of the mean) were propagated from subgroup standard errors using the rule for weighted sums.

At treeline, any benefits of water addition to fourth-year limber pine recruitment were contingent on heating, with benefits in unheated but not heated plots (Tables 5 and S4).

#### Provenance effects

Contrary to our expectation that seeds would be locally adapted, the low-elevation seed provenance had greater first-year recruitment than the high-elevation provenance for both Engelmann spruce and limber pine, at *all* sites (Tables 2, 3, S1 and S2). For Engelmann spruce, the biggest differences were at the forest and alpine sites, where low-provenance recruitment was roughly double that of high (Fig. 2e), with a smaller provenance effect at the treeline site (Table S1). For limber pine, the provenance effects were similar across

sites (Fig. 2f). The Engelmann spruce high-elevation provenance disadvantage was not significant at any site for older seedling survival ( $P > 0.07$ ; Tables S5, S7, S9), and cumulative fourth-year recruitment was not significantly different between provenances at treeline or alpine sites (Tables 4 and S3). As limber pine seedlings matured, the high-provenance disadvantage persisted, with worse first- to second- and second- to third-year survival at treeline ( $P < 0.03$ ; Tables S6 and S8), and with 70.4%, 57.8%, and 71.3% less fourth-year recruitment in forest, treeline, and alpine sites, respectively (Tables 5 and S4).

Provenances initially responded similarly to warming and watering, with no significant provenance by treatment interactions for first-year recruitment of either species (Tables 2, 3, S1, S2). For limber pine establishing in the forest, heating diminished the

**Table 4** Generalized linear mixed effects model likelihood ratio tests (LRT) and  $P$ -values,  $P(\chi^2)$ , for main effects and all two-way interactions on fourth-year recruitment of Engelmann spruce

Engelmann spruce Seed to fourth year	Treeline		Alpine	
	LRT (df)	$P(\chi^2)$	LRT (df)	$P(\chi^2)$
Heat	4.51 (1)	<b>0.034</b>	4.27 (1)	<b>0.039</b>
Water	3.33 (1)	0.068	0.21 (1)	0.65
Provenance	1.55 (1)	0.21	2.65 (1)	0.10
Cohort	39.18 (1)	<b>&lt;10<sup>-5</sup></b>	8.07 (1)	<b>0.0045</b>
Heat × water	0.96 (1)	0.33	1.01 (1)	0.31
Heat × provenance	0.16 (1)	0.69	0.14 (1)	0.71
Heat × cohort	7.74 (1)	<b>0.0054</b>	3.34 (1)	0.068
Water × provenance	0.36 (1)	0.55	0.14 (1)	0.71
Water × cohort	0.21 (1)	0.65	1.70 (1)	0.19
Provenance × cohort	2.65 (1)	0.10	0.91 (1)	0.34

There are no values for forest because only five plots had survivors to their fourth year – all in the control and watered groups. Random effects variances (for treeline and alpine, respectively) are 0.48 and 0.17 for plot and 0.36 and 1.93 for the observation-level random effect.  $P < 0.05$  are given in bold type. All parameter estimates are given in Table S3.

low-provenance advantage (a negative interaction), while in the alpine, the low-provenance advantage was enhanced by heating (Tables 5 and S4). These effects emerged with first- to second-year survival in the alpine and with second- to third-year survival in the forest (Tables S6 and S8). At treeline, watering diminished the low-provenance advantage in first- to second-year survival of limber pine ( $P = 0.020$ ; Table S6), but this effect did not persist to the fourth year.

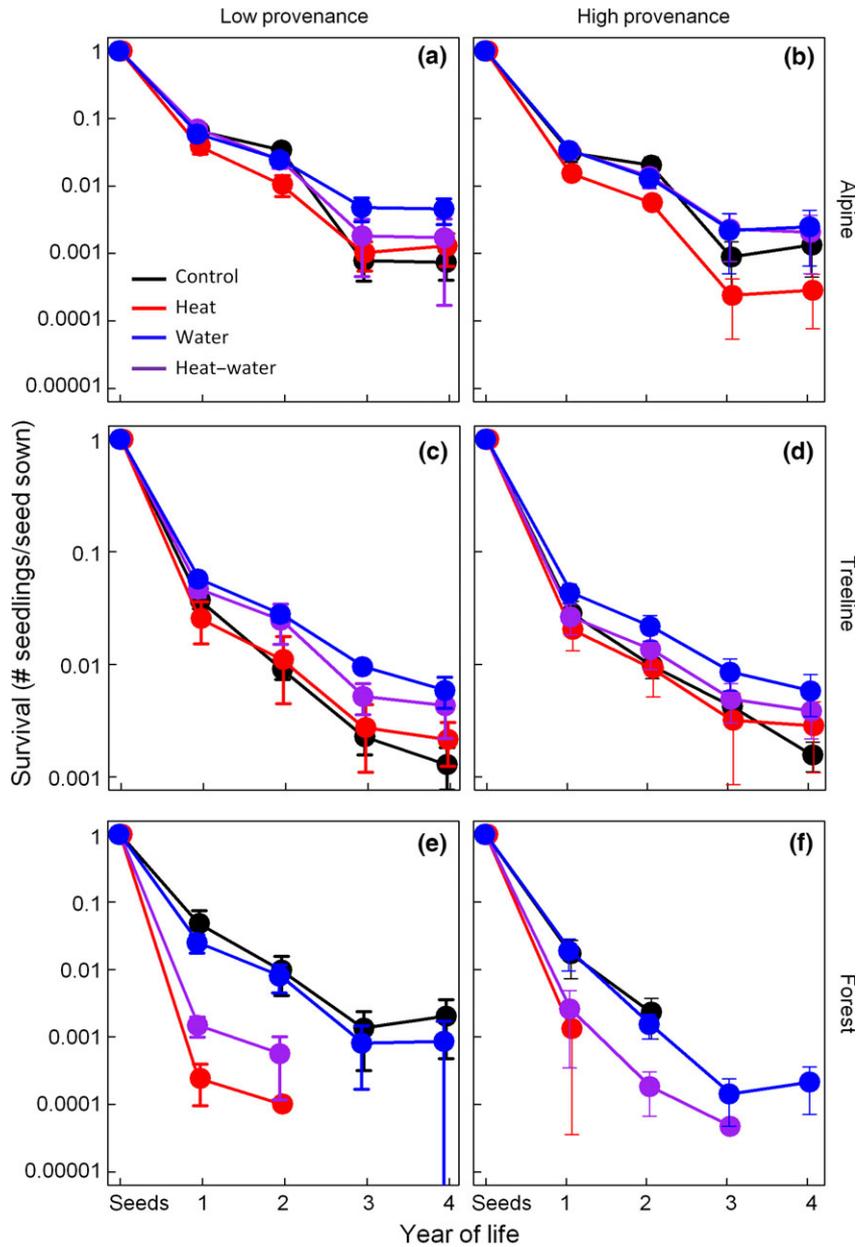
## Discussion

Our results suggest that high-elevation mountain forests with water-limited growing seasons, such as in Western North America, are likely to experience recruitment declines or, at best, no new advantage as climate warms, growing seasons lengthen, and evaporative demand increases. Recruitment declines with warming are the opposite of what is required to compensate for increasing adult mortality in Western U.S. forests (Van Mantgem *et al.*, 2009; Williams *et al.*, 2013; Smith *et al.*, 2015). While warming decreased recruitment across all sites for Engelmann spruce, dramatic reductions at the forest site (Fig. 2) likely reflect greater realized experimental warming in this site, which had lower wind speeds and therefore greater increases in soil and plant temperatures with infrared heating (Table 1). We did not test whether tree seedlings establishing at treeline and alpine sites would experience similarly dramatic reductions with temperature

increases comparable to those in the forest. However, the fact that modest warming (1–2 °C) reduced spruce recruitment at and above treeline highlights the sensitivity of this species. Decreased Engelmann spruce recruitment with warming is consistent with reported reductions in seed germination at high temperatures and at low moisture (Kaufmann & Eckard, 1977) and with a negative correlation between temperature and radial growth for mature Engelmann spruce in dry sites over the period 1899–1991 (Villalba *et al.*, 1994).

Contrary to our expectations, negative effects of warming can even affect recruitment in sites at and above treeline. Previous studies at treeline have found preferential seedling survival in microsites protected from frost (Maher *et al.*, 2005; Maher & Germino, 2006) and that passive nighttime warming can alleviate low temperature stress and increase seedling survival (Germino & Smith, 1999; Batllori *et al.*, 2009). Unlike studies using open-top chambers, which can cool at night (Danby & Hik, 2007) by limiting convective warming of the surface (reducing sensible heat flux from the air to the surface), infrared heaters raise temperatures during the day and night. Therefore, the negative effects of heating that we observed are not due to unexpected nighttime cooling in heated plots at treeline or in the alpine. While Harsch *et al.* (2009) found that many alpine treelines have been advancing upslope in response to historical warming, they also found that nearly half have not, suggesting other factors may constrain responses to temperature trends in many sites. Winter damage and low temperature photoinhibition during the growing season have been identified as factors limiting tree establishment even in the presence of warming (reviewed in Harsch & Bader, 2011).

Moisture limitation, and an attendant lack of evaporative cooling, should be considered a significant constraint to recruitment even at and beyond upper treeline. In our experiment, heating decreased soil moisture (Table 1), likely exacerbating moisture stress during germination and initial establishment. First-year limber pine recruitment increased with greater surface soil moisture and shorter growing seasons (Moyes *et al.*, 2013), with second-year seedling carbon assimilation roughly equally limited by temperature and moisture at treeline (Moyes *et al.*, 2015). While warming does alleviate low temperature stress early and late in the growing season in our alpine and treeline sites, warming throughout the growing season appears to counteract this benefit by enhancing moisture stress (Moyes *et al.*, 2015). Further, we found that adding summer moisture increases Engelmann spruce first-year recruitment across all sites and limber pine fourth-year recruitment in the forest. These results are corroborated by a precipitation manipulation



**Fig. 3** Engelmann spruce seedling survival curves. Recruitment to year four on a log scale for Engelmann spruce low-provenance (a, c, e) and high-provenance (b, d, f) seeds across sites and treatments. Points are mean survival calculated across the years for which data are available (lines end when there are no survivors). Error bars are standard errors of the means, calculated from plot-level averages, across years. For most first-year recruitment values, error bars are too small to be seen. For older seedlings, when only one plot had survivors, there are no error bars.

experiment conducted in a subalpine meadow in Utah, which found that over-summer Engelmann spruce seedling survival was best correlated with soil moisture (Gill *et al.*, 2015). Notably, watering had no effect on limber pine recruitment at the treeline site (Tables 3 and 5), where recruitment was strongest overall (Figs 2 and 4), and where snow melt is latest and the growing season is shortest (Table 1). We hypothesize that warming increased seedling mortality risk by lengthening the

growing season and reducing near-surface moisture, elevating incidence of hydraulic failure in sensitive new germinants, and by degrading seedling carbon balance via increased respiration and reduced carbon assimilation, even in normal precipitation years.

For the Rocky Mountains, we have experimentally shown that summer moisture may provide an additional constraint to tree establishment at and above treeline and that warming may exacerbate, rather than

**Table 5** Generalized linear mixed effects model likelihood ratio tests (LRT) and  $P$ -values,  $P(\chi^2)$ , for main effects and all two-way interactions on fourth-year recruitment of limber pine

Limber pine Seed to fourth year	Forest		Treeline		Alpine	
	LRT (df)	$P(\chi^2)$	LRT (df)	$P(\chi^2)$	LRT (df)	$P(\chi^2)$
Heat	2.80 (1)	0.094	0.93 (1)	0.34	0.00 (1)	0.98
Water	11.83 (1)	<b>0.00058</b>	0.34 (1)	0.56	2.42 (1)	0.12
Provenance	33.85 (1)	$<10^{-5}$	43.98 (1)	$<10^{-5}$	58.26 (1)	$<10^{-5}$
Cohort	16.64 (1)	$4.5 \times 10^{-5}$	133.36 (1)	$<10^{-5}$	65.07 (1)	$<10^{-5}$
Heat $\times$ water	4.67 (1)	<b>0.031</b>	6.30 (1)	<b>0.012</b>	0.03 (1)	0.86
Heat $\times$ provenance	6.05 (1)	<b>0.014</b>	0.21 (1)	0.65	7.52 (1)	<b>0.0061</b>
Heat $\times$ cohort	2.21 (1)	0.14	2.10 (1)	0.15	0.59 (1)	0.44
Water $\times$ provenance	0.92 (1)	0.34	0.26 (1)	0.61	3.83 (1)	0.050
Water $\times$ cohort	0.18 (1)	0.67	2.24 (1)	0.13	3.10 (1)	0.078
Provenance $\times$ cohort	17.21 (1)	$3.3 \times 10^{-5}$	10.84 (1)	<b>0.00099</b>	16.35 (1)	$5.3 \times 10^{-5}$

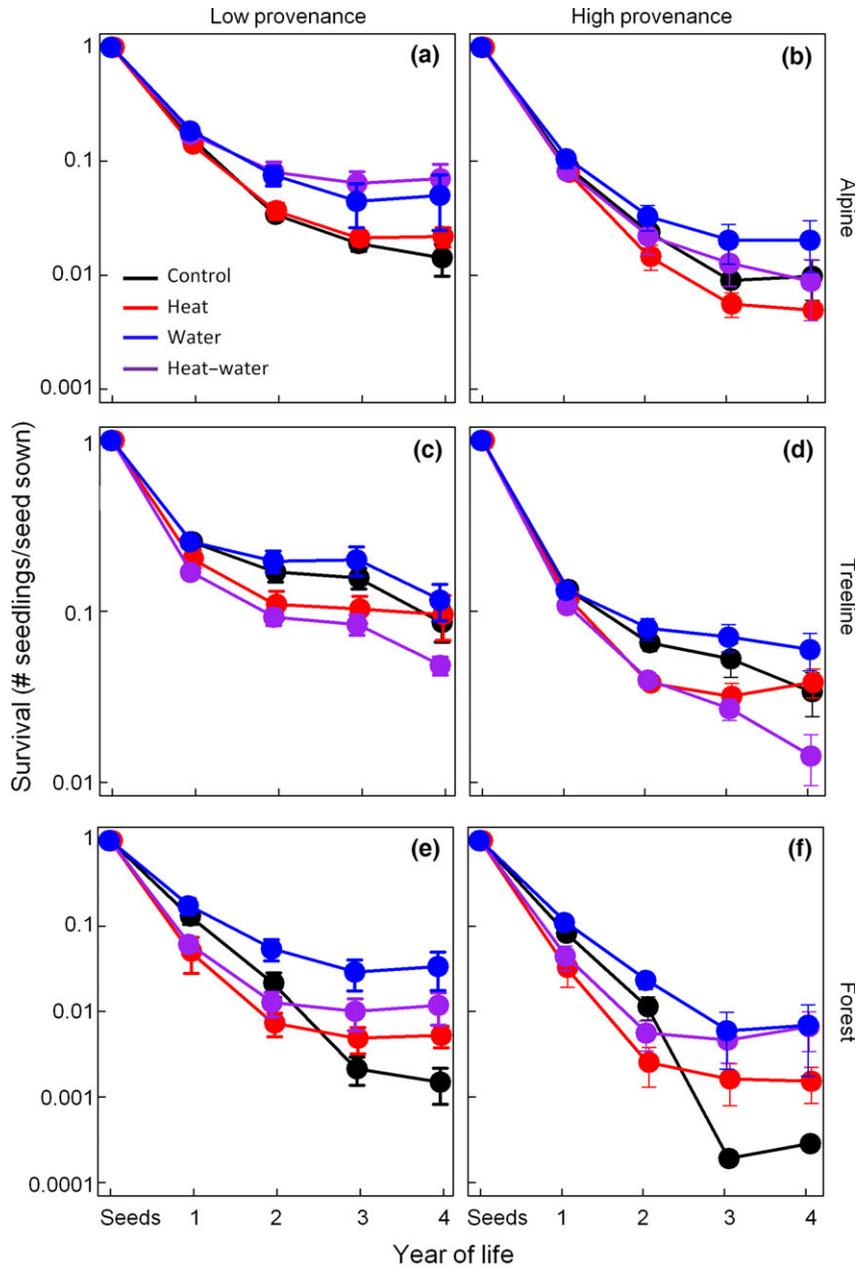
Random effects variances (for forest, treeline, and alpine, respectively) are 0.78, 0.11, and 0.44 for plot, and 0.21, 0.46, and 0.21 for the observation-level random effect.  $P < 0.05$  are given in bold type. All parameter estimates are given in Table S4.

ameliorate, this constraint. Our results for seedlings are qualitatively consistent with observations and predictions of increased adult tree mortality in response to water stress (Van Mantgem *et al.*, 2009; Williams *et al.*, 2013; McDowell & Allen, 2015), and with positive correlations between precipitation and radial growth (Vilalba *et al.*, 1994) for adult subalpine trees, but reveal quantitatively greater impacts on vital rates for these more sensitive, younger life stages (Dobrowski *et al.*, 2015). While Western North America is known to have water-limited growing seasons, warming will lengthen mountain growing seasons and increase evaporative demand everywhere, potentially altering the recruitment environment beyond recent historical conditions in mountain ranges worldwide.

The greater initial (first year) Engelmann spruce response to watering may help explain species differences in response to warming. Because limber pine seeds and emergent seedlings are much larger and have deeper roots than emergent Engelmann spruce seedlings, limber pine may be better able to withstand the drying that accompanies warming and benefit sooner from warming at high elevations. Limber pine first-year recruitment was much greater than Engelmann spruce recruitment overall (note  $y$ -axis labels on Fig. 2), and limber pine seedlings that survived the first year then were unaffected or benefitted from heating (and watering) in later years. Conversely, Engelmann spruce seedlings did not see any benefit from heating at any site. Consistent with our findings, niche model projections using forest inventory data across the Western United States point to greater recruitment declines in Engelmann spruce than limber pine with warming (Dobrowski *et al.*, 2015). Differences in species responses to warming and water stress suggest a

potential for shifts in high-elevation forest composition, similar to past climate-driven reorganization of plant communities (Le Roux & McGeoch, 2008). In particular, tree species that successfully establish above current treeline may differ from those that are currently abundant in upper elevation forests. While limber pine is currently a minor component of the forest and treeline communities in Colorado, future warming could provide it a competitive advantage within the forest and in colonizing alpine tundra. Ultimately, future forest composition will also depend on the growth, mortality, and reproductive responses of established trees to climate change, and on species interactions that could change as trees and forest stands mature, and as the environment changes (Boyden *et al.*, 2009; Gómez-Aparicio *et al.*, 2011; Ettinger & Hille Ris Lambers, 2013).

Reorganization of forest communities may be accompanied by changes in the genetic structure of populations. Unexpectedly, the low-elevation provenance had greater recruitment across all sites, including the alpine site, suggesting a clear advantage for low-elevation genotypes, at least at this early life stage. It is not clear why the low provenance generally had higher recruitment. High-provenance seeds were not consistently smaller or less viable than low-provenance seeds but may have differed in less apparent ways due to different maternal environments. Low-provenance seedlings seemed to emerge earlier than high-provenance seedlings, enabling a longer first growing season, although longer growing seasons may not favor survival (Moyes *et al.*, 2013). Low-provenance seedlings also have greater photosynthesis and carbon balance (photosynthesis/respiration) than high-provenance seedlings (Reinhardt *et al.*, 2011). These phenological and physiological differences may reflect a more rapid,



**Fig. 4** Limber pine seedling survival curves. Recruitment to year four on a log scale for limber pine low-provenance (a, c, e) and high-provenance (b, d, f) seeds across sites and treatments. Points are mean survival calculated across the years for which data are available. Error bars are standard errors of the means, calculated from plot-level averages, across years. For most first-year recruitment values, error bars are too small to be seen. For older seedlings, when only one plot had survivors, there are no error bars.

competitive growth strategy yielding more robust low-provenance seedlings regardless of site. In this region, which is largely snow melt-driven (Hu *et al.*, 2010), earlier snow melt is often accompanied by earlier water stress, which frequently is not ameliorated until consistent monsoon precipitation in July and August. Early emergence and high assimilation and growth rates may help low-provenance seedlings avoid desiccation. It is also possible that over the 5 years of our study, climatic

conditions happened to be favorable for the low-elevation provenance and that a series of years with less favorable conditions (e.g., frequent summer frost) could have favored the high provenance at high elevations. However, recent warming and associated changes in growing season length (Clow, 2010; Oyler *et al.*, 2015) may have already made treeline and alpine sites more climatically similar to lower elevation sites of the past, making adaptations for tolerating low temperature

(e.g., frost during the growing season) less advantageous now and in the future. For limber pine, heating enhanced the low-provenance advantage in the alpine site, suggesting that future population establishment in the alpine could depend, in part, on the origin of dispersed seed. More work is needed to assess whether the provenance differences we observed in seedlings are maintained in older trees, which may have additional provenance-specific climate sensitivities (McLane *et al.*, 2011).

Greater recruitment of the low-elevation provenance at high elevations has important implications for forest range shifts. If high-elevation seed, which is most readily available for colonizing alpine and treeline sites, has lower recruitment, tree migration into the alpine will be slowed. At the same time, if low-elevation tree mortality continues to increase (Smith *et al.*, 2015), and if this reduces the number of reproductive trees, the degree of gene flow between high- and low-elevation populations may become an important constraint to rates of migration. Alternately, if gene flow from low elevations can increase the performance of high-elevation seed sources over time, keeping up with climate change, then adaptation and upslope range expansion may accelerate over time (Alberto *et al.*, 2013). More work is needed to understand factors limiting gene flow among populations along elevation gradients, including whether climate change can alter historical constraints such as mismatched reproductive phenology (Schuster *et al.*, 1989). While previous studies have highlighted the importance of climatically adapted genotypes to predictions of future tree distributions and forest productivity (Wang *et al.*, 2010; Valladares *et al.*, 2014), they have typically assumed that adult tree traits are predictive of demographic outcomes and neglected traits shaping the regeneration niche (Grubb, 1977). Such regeneration traits may be critical for determining the pace of range shifts with climate change.

Understanding the sensitivity of young life stages to climate is critically important for projecting the impact of climate change on tree populations and distributions. The climate and provenance effects described here emerged across years that varied substantially in snow melt timing and summer rainfall, and occurred within a forest thought to be maintained by continuous replacement rather than episodic recruitment (Knowles & Grant, 1983). Therefore, given (i) observed increases in mature tree mortality in the forest (Smith *et al.*, 2015), (ii) a clear and large negative effect of warming on seedling recruitment in the forest, and (iii) a negative effect of warming on seedling recruitment above treeline, we expect the elevational range of Engelmann spruce to contract in the coming centuries. Limber pine appears better able to persist within its current range

and expand upslope due to compensating positive and negative effects of warming on recruitment in the alpine and in the forest. To quantitatively estimate the consequences of climate-limited recruitment for forest tree population sizes and rates of migration requires integration of our experimental results with data on tree growth, mortality, seed production, and dispersal in spatially explicit demographic models. Such models would also enable us to explore whether episodically favorable conditions within the long lifetime of these species could overwhelm the shifts in mean conditions that we describe here and thereby maintain existing populations or enable an abrupt upslope expansion. Further work is also needed to determine whether climate sensitivities and provenance differences are consistent across life stages, to quantify the climate sensitivities of co-occurring species, and to assess how changing forest composition will affect high-elevation biodiversity and ecosystem function.

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### References

- Alberto FJ, Aitken SN, Alia R *et al.* (2013) Potential for evolutionary responses to climate change – evidence from tree populations. *Global Change Biology*, **19**, 1645–1661.
- Batllori E, Camarero JJ, Ninot JM, Gutiérrez E (2009) Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to climate warming. *Global Ecology and Biogeography*, **18**, 460–472.
- Boyden SB, Reich PB, Puettmann KJ, Baker TR (2009) Effects of density and ontogeny on size and growth ranks of three competing tree species. *Journal of Ecology*, **97**, 277–288.
- Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag New York Inc, New York, NY.
- Castanha C, Torn MS, Germino MJ, Weibel B, Kueppers LM (2013) Conifer seedling recruitment across a gradient from forest to alpine tundra: effects of species, provenance, and site. *Plant Ecology & Diversity*, **6**, 307–318.
- Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.
- Crow DW (2010) Changes in the timing of snowmelt and streamflow in Colorado: a response to recent warming. *Journal of Climate*, **23**, 2293–2306.
- Crimmins SM, Dobrowski SZ, Greenberg JA, Abatzoglou JT, Mynsberge AR (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, **331**, 324–327.
- Danby RK, Hik DS (2007) Responses of white spruce (*Picea glauca*) to experimental warming at a subarctic alpine treeline. *Global Change Biology*, **13**, 437–451.
- Dobrowski SZ, Swanson AK, Abatzoglou JT, Holden ZA, Safford HD, Schwartz MK, Gavin DG (2015) Forest structure and species traits mediate projected recruitment declines in western US tree species. *Global Ecology and Biogeography*, **24**, 917–927.
- Ettinger AK, Hille Ris Lambers J (2013) Climate isn't everything: competitive interactions and variation by life stage will also affect range shifts in a warming world. *American Journal of Botany*, **100**, 1344–1355.

- Fellows AW, Goulden ML (2012) Rapid vegetation redistribution in Southern California during the early 2000s drought. *Journal of Geophysical Research: Biogeosciences*, **117**, 2156–2202.
- Frost GV, Epstein HE (2014) Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. *Global Change Biology*, **20**, 1264–1277.
- Germino MJ, Smith WK (1999) Sky exposure, crown architecture, and low-temperature photoinhibition in conifer seedlings at alpine treeline. *Plant, Cell and Environment*, **22**, 407–415.
- Gill RA, Campbell CS, Karlinsky SM (2015) Soil moisture controls Engelmann spruce (*Picea engelmannii*) seedling carbon balance and survivorship at timberline in Utah, USA. *Canadian Journal of Forest Research*, **45**, 1845–1852.
- Gómez-Aparicio L, García-Valdés R, Ruíz-Benito P, Zavala MA (2011) Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. *Global Change Biology*, **17**, 2400–2414.
- Gottfried M, Pauli H, Futschik A *et al.* (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, **2**, 111–115.
- Grau O, Ninot JM, Cornelissen JHC, Callaghan TV (2013) Similar tree seedling responses to shrubs and to simulated environmental changes at Pyrenean and subarctic treelines. *Plant Ecology & Diversity*, **6**, 329–342.
- Grubb PJ (1977) Maintenance of species-richness in plant communities – importance of regeneration niche. *Biological Reviews of the Cambridge Philosophical Society*, **52**, 107–145.
- Harsch MA, Bader MY (2011) Treeline form – a potential key to understanding treeline dynamics. *Global Ecology and Biogeography*, **20**, 582–596.
- Harsch MA, Hulme PE, Mcglone MS, Duncan RP (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, **12**, 1040–1049.
- Harte J, Torn M, Chang F-R, Feifarek B, Kinzig A, Shaw R, Shen K (1995) Global warming and soil microclimate: results from a meadow-warming experiment. *Ecological Applications*, **5**, 132–150.
- Hu JIA, Moore DJP, Burns SP, Monson RK (2010) Longer growing seasons lead to less carbon sequestration by a subalpine forest. *Global Change Biology*, **16**, 771–783.
- Ibanez I, Clark JS, Ladeau S, Hillerislambers J (2007) Exploiting temporal variability to understand tree recruitment response to climate change. *Ecological Monographs*, **77**, 163–177.
- Kaufmann MR, Eckard AN (1977) Water potential and temperature effects on germination of Engelmann spruce and Lodgepole pine seeds. *Forest Science*, **23**, 27–33.
- Kimball BA, Conley MM, Wang S, Lin X, Luo C, Morgan J, Smith D (2008) Infrared heater arrays for warming ecosystem field plots. *Global Change Biology*, **14**, 309–320.
- Kittel TGF, Williams MW, Chowanski K, Hartman M, Ackerman T, Losleben M, Blanken PD (2015) Contrasting long-term alpine and subalpine precipitation trends in a mid-latitude North American mountain system, Colorado Front Range, USA. *Plant Ecology & Diversity*, **8**, 607–624.
- Knowles P, Grant MC (1983) Age and size structure analyses of Engelmann spruce, Ponderosa pine, Lodgepole pine, and Limber pine in Colorado. *Ecology*, **64**, 1–9.
- Korner C (2012) *Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits*. Springer, Basel.
- Kremer A, Ronce O, Robledo-Arnuncio JJ *et al.* (2012) Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecology Letters*, **15**, 378–392.
- Le Roux PC, McGeoch MA (2008) Rapid range expansion and community reorganization in response to warming. *Global Change Biology*, **14**, 2950–2962.
- Lenoir J, Gégout JC, Marquet PA, De Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768–1771.
- Lenoir J, Gégout J-C, Pierrat J-C, Bontemps J-D, Dhôte J-F (2009) Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). *Ecography*, **32**, 765–777.
- Lenoir J, Gégout J-C, Guisan A *et al.* (2010) Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, **33**, 295–303.
- Loranger H, Zotz G, Bader MY (2016) Early establishment of trees at the alpine treeline: idiosyncratic species responses to temperature-moisture interactions. *AoB Plants*, **8**, plw053. doi: 10.1093/aobpla/plw053
- Maher EL, Germino MJ (2006) Microsite differentiation among conifer species during seedling establishment at alpine treeline. *Ecoscience*, **13**, 334–341.
- Maher EL, Germino MJ, Hasselquist NJ (2005) Interactive effects of tree and herb cover on survivorship, physiology, and microclimate of conifer seedlings at the alpine tree-line ecotone. *Canadian Journal of Forest Research*, **35**, 567–574.
- Malanson GP, Butler DR, Fagre DB *et al.* (2007) Alpine treeline of western North America: linking organism-to-landscape dynamics. *Physical Geography*, **28**, 378–396.
- McDowell NG, Allen CD (2015) Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change*, **5**, 669–672.
- McLane SC, Daniels LD, Aitken SN (2011) Climate impacts on lodgepole pine (*Pinus contorta*) radial growth in a provenance experiment. *Forest Ecology and Management*, **262**, 115–123.
- Mclaughlin BC, Zavaleta ES (2012) Predicting species responses to climate change: demography and climate microrefugia in California valley oak (*Quercus lobata*). *Global Change Biology*, **18**, 2301–2312.
- Meromy L, Molotch NP, Williams MW, Musselman KN, Kueppers LM (2015) Snow-pack-climate manipulation using infrared heaters in subalpine forests of the Southern Rocky Mountains, USA. *Agricultural and Forest Meteorology*, **203**, 142–157.
- Millar CI, Westfall RD, Delany DL, Flint AL, Flint LE (2015) Recruitment patterns and growth of high-elevation pines in response to climatic variability (1883–2013), in the western Great Basin, USA. *Canadian Journal of Forest Research*, **45**, 1299–1312.
- Mitton JB (1995) Genetics and the physiological ecology of conifers. In: *Ecophysiology of Coniferous Forests* (eds Smith WK, Hinchley TM), pp. 1–36. Academic Press, Inc., San Diego, CA.
- Monahan WB, Cook T, Melton F, Connor J, Bobowski B (2013) Forecasting distributional responses of limber pine to climate change at management-relevant scales in Rocky Mountain National Park. *PLoS One*, **8**, e83163.
- Morgan C, Losey A, Trout L (2014) Late-Holocene paleoclimate and treeline fluctuation in Wyoming's Wind River Range, USA. *The Holocene*, **24**, 209–219.
- Moritz C, Agudo R (2013) The future of species under climate change: resilience or decline? *Science*, **341**, 504–508.
- Moyes AB, Castanha C, Germino MJ, Kueppers LM (2013) Warming and the dependence of limber pine (*Pinus flexilis*) establishment on summer soil moisture within and above its current elevation range. *Oecologia*, **171**, 271–282.
- Moyes AB, Germino MJ, Kueppers LM (2015) Moisture rivals temperature in limiting photosynthesis by trees establishing beyond their cold-edge range limit under ambient and warmed conditions. *New Phytologist*, **207**, 1005–1014.
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142.
- Oyler JW, Dobrowski SZ, Ballantyne AP, Klene AE, Running SW (2015) Artificial amplification of warming trends across the mountains of the western United States. *Geophysical Research Letters*, **42**, 153–161.
- Pauli H, Gottfried M, Dullinger S *et al.* (2012) Recent plant diversity changes on Europe's mountain summits. *Science*, **336**, 353–355.
- Rehfeldt GE, Ying CC, Spittlehouse DL, Hamilton DA Jr (1999) Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. *Ecological Monographs*, **69**, 375–407.
- Rehfeldt GE, Crookston NL, Warwell MV, Evans JS (2006) Empirical analyses of plant-climate relationships for the western United States. *International Journal of Plant Sciences*, **167**, 1123–1150.
- Rehm EM, Feeley KJ (2015) The inability of tropical cloud forest species to invade grasslands above treeline during climate change: potential explanations and consequences. *Ecography*, **38**, 1167–1175.
- Reinhardt K, Castanha C, Germino MJ, Kueppers LM (2011) Ecophysiological variation in two provenances of *Pinus flexilis* seedlings across an elevation gradient from forest to alpine. *Tree Physiology*, **31**, 615–625.
- Rossi S, Deslauriers A, Grisar J *et al.* (2008) Critical temperatures for xylogenesis in conifers of cold climates. *Global Ecology and Biogeography*, **17**, 696–707.
- Salzer MW, Hughes MK, Bunn AG, Kipfmüller KF (2009) Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proceedings of the National Academy of Sciences*, **106**, 20348–20353.
- Schuster WS, Alles DL, Mitton JB (1989) Gene flow in limber pine – evidence from pollination phenology and genetic differentiation along an elevational transect. *American Journal of Botany*, **76**, 1395–1403.
- Schwoerer C, Henne PD, Tinner W (2014) A model-data comparison of Holocene timberline changes in the Swiss Alps reveals past and future drivers of mountain forest dynamics. *Global Change Biology*, **20**, 1512–1526.
- Smith WK, Germino MJ, Johnson DM, Reinhardt K (2009) The altitude of alpine treeline: a bellwether of climate change effects. *The Botanical Review*, **75**, 163–190.
- Smith JM, Paritsis J, Veblen TT, Chapman TB (2015) Permanent forest plots show accelerating tree mortality in subalpine forests of the Colorado Front Range from 1982 to 2013. *Forest Ecology and Management*, **341**, 8–17.
- Stephenson NL, Das AJ (2011) Comment on “changes in climatic water balance drive downhill shifts in plant species' optimum elevations”. *Science*, **334**, 177.

- Tingstad L, Olsen SL, Klanderud K, Vandvik V, Ohlson M (2015) Temperature, precipitation and biotic interactions as determinants of tree seedling recruitment across the tree line ecotone. *Oecologia*, **179**, 599–608.
- Valladares F, Matesanz S, Guilhaumon F *et al.* (2014) The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters*, **17**, 1351–1364.
- Van de Ven CM, Weiss SB, Ernst WG (2007) Plant species distributions under present conditions and forecasted for warmer climates in an arid mountain range. *Earth Interactions*, **11**, 9.
- Van Mantgem PJ, Stephenson NL, Byrne JC *et al.* (2009) Widespread increase of tree mortality rates in the western United States. *Science*, **323**, 521–524.
- Villalba R, Veblen TT, Ogden J (1994) Climatic influences on the growth of subalpine trees in the Colorado Front Range. *Ecology*, **75**, 1450–1462.
- Walck JL, Hidayati SN, Dixon KW, Thompson K, Poschlod P (2011) Climate change and plant regeneration from seed. *Global Change Biology*, **17**, 2145–2161.
- Wang T, O'neill GA, Aitken SN (2010) Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecological Applications*, **20**, 153–163.
- Williams PA, Allen CD, Macalady AK *et al.* (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, **3**, 292–297.
- Zhu K, Woodall CW, Clark JS (2012) Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology*, **18**, 1042–1052.
- Zurbriggen N, Hättenschwiler S, Frei ES, Hagedorn F, Bebi P (2013) Performance of germinating tree seedlings below and above treeline in the Swiss Alps. *Plant Ecology*, **214**, 385–396.

## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Generalized linear mixed effects model parameter estimates for main effects and all two-way interactions on first-year recruitment of Engelmann spruce.

**Table S2.** Generalized linear mixed effects model parameter estimates for main effects and all two-way interactions on first-year recruitment of limber pine.

**Table S3.** Generalized linear mixed effects model parameter estimates for main effects and all two-way interactions on fourth-year recruitment of Engelmann spruce.

**Table S4.** Generalized linear mixed effects model parameter estimates for main effects and all two-way interactions on fourth-year recruitment of limber pine.

**Table S5.** Generalized linear mixed effects model parameter estimates for main effects and all two-way interactions on first to second-year survival of Engelmann spruce.

**Table S6.** Generalized linear mixed effects model parameter estimates for main effects and all two-way interactions on first to second-year survival of limber pine.

**Table S7.** Generalized linear mixed effects model parameter estimates for main effects and all two-way interactions on second to third-year survival of Engelmann spruce.

**Table S8.** Generalized linear mixed effects model parameter estimates for main effects and all two-way interactions on second to third-year survival of limber pine.

**Table S9.** Generalized linear mixed effects model parameter estimates for main effects and all two-way interactions on third to fourth-year survival of Engelmann spruce.

**Table S10.** Generalized linear mixed effects model parameter estimates for main effects and all two-way interactions on third to fourth-year survival of limber pine.

**Table S11.** Marginal (fixed factors only) and conditional (all factors)  $R^2$  values for the models presented in Tables S1–S10.