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Title Page

Title: Seed origin and warming constrain lodgepole pine recruitment, slowing the pace of

population range shifts

Running head: Provenance and warming limit pine populations

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Abstract

Understanding how climate warming will affect the demographic rates of different ecotypes

is critical to predicting shifts in species distributions. Here we present results from a common

garden, climate change experiment in which we measured seedling recruitment of lodgepole

pine, a widespread North American conifer that is also planted globally. Seeds from a low-

elevation provenance had greater recruitment to their third year (by 323%) than seeds from a

high-elevation provenance across sites within and above its native elevation range and across

climate manipulations. Heating reduced (by 49%) recruitment to the third year of both low-

and high-elevation seed sources across the elevation gradient, while watering alleviated some

of the negative effects of heating (108% increase in watered plots). Demographic models

based on recruitment data from the climate manipulations and long-term observations of adult

populations revealed that heating could effectively halt modeled upslope range expansion

except when combined with watering. Simulating fire and rapid post-fire forest recovery at

lower elevations accelerated lodgepole pine expansion into the alpine, but did not alter final

abundance rankings among climate scenarios. Regardless of climate scenario, greater

recruitment of low-elevation seeds compensated for longer dispersal distances to treeline,

assuming colonization was allowed to proceed over multiple centuries. Our results show that

ecotypes from lower elevations within a species' range could enhance recruitment and

facilitate upslope range shifts with climate change.

Introduction

Climate change is altering the environment for tree recruitment, growth, and survival, with the potential to alter population sizes, distributions and genotypic variation across populations. In the Western United States, recent trends and projections indicate warmer, drier conditions (Seager *et al.*, 2007; Dai, 2013) that are already altering forest structure (Allen *et al.*, 2010; Williams *et al.*, 2013). Drought-induced adult mortality (van Mantgem *et al.*, 2009; McDowell & Allen, 2015), higher incidence of fire in Western US forests (Abatzoglou & Williams, 2016; Westerling, 2016), and lower tree recruitment under heating (Kueppers *et al.*, 2017) all point to a restructuring of forest ecosystems in response to changing climate. Forest restructuring depends on and affects genetic variation across populations, and can facilitate local adaptation to the new climate (Davis *et al.*, 2005; Aitken *et al.*, 2008; Alberto *et al.*, 2013).

For widespread tree species, fine-scale climate heterogeneity structures the ecotypic variation that in turn drives demographic rates and population sizes (Schuster *et al.*, 1989; Aitken *et al.*, 2008; Wang *et al.*, 2010). Ecotypic variation has been linked to environmentally mediated differences in gene frequencies across latitude and elevation gradients (Schuster *et al.*, 1989; Mitton, 1995; Mitton & Duran, 2004; Jump *et al.*, 2006; Mosca *et al.*, 2012), with important implications for growth and survival. Despite having wind-dispersed pollen, population-level variation in conifers can be preserved across elevation gradients due to asynchrony between pollen release and megastrobilus receptivity across elevations (Schuster *et al.*, 1989). In common garden experiments across western Canada, populations of lodgepole pine (*Pinus contorta*) were found to have steep clinal variation, with the majority of populations occurring at locally optimal sites (Wu & Ying, 2004), even if sites were sub-optimal relative to lodgepole pine's entire range (Rehfeldt *et al.*, 1999). Local climate adaptation is important to range shifts because ecotypes must shift with

climate to maintain the demographic rates that have led to current populations. If existing populations receive no influx of warm-adapted ecotypes, 20-year growth and survival rates of lodgepole in British Columbia are expected to be at least 10% lower than they are now (Rehfeldt *et al.*, 1999), with bigger declines (30-40%) at lower elevations and latitudes (i.e. at the warmest sites within the species' range). Further, comparisons of different subspecies of lodgepole pine (*latifolia* versus *contorta*) demonstrate that different ecotypes and provenances can have different growth and survival responses to deviations from their climatic optimum (Rehfeldt *et al.*, 1999), with mal-adapted populations (e.g. cold-adapted individuals in warm locations or vice-versa) showing the highest sensitivities to small changes in climate (McLane *et al.*, 2011). Common garden experiments with other pines show similar intraspecific variation. Genetic variability in Scots pine (*Pinus sylvestris*) and maritime pine (*Pinus pinaster*) led to survival differences between populations (Benito Garzón *et al.*, 2011), with Scots pine survival rates decreasing with climatic distance between the source population and the trial sites (Reich & Oleksyn, 2008). Scots pine also demonstrated climate-mediated genetic variation in physiology (Reich *et al.*, 1996). What is missing is a better understanding of whether ecotypes respond differently to *in situ* climate change.

Population responses at range margins may dictate overall species' responses to climate change (Hampe & Petit, 2005); the cold-edge margin will be an important source of propagules for the colonization front and the warm-edge margin will be an important source of warm-adapted genotypes. Migration from warm-edge range margins to range centers goes against the assumed outward flow of propagules from a globally optimal range center (Savolainen *et al.*, 2007; Alberto *et al.*, 2013). However, in moving poleward and to higher elevations, with rapid climate change, nearby sites may warm beyond the climatic niche of a particular ecotype, requiring warm-adapted ecotypes to move long-distances, potentially

"leap-froging" cold-adapted ecotypes. Because seed rain decreases sharply with distance, there are trade-offs among dispersal distance, priority effects, and relative ecotypic fitness. In high-elevation, topographically heterogeneous environments, we need a quantitative understanding of how this trade-off structures forests responding to climate change.

The demographic processes that drive shifts in species' ranges and gene flow have been largely neglected when projecting the impacts of climate change (Urban *et al.*, 2016). Dynamic population models (Dullinger *et al.*, 2012, 2015; Conlisk *et al.*, 2013; Fordham *et al.*, 2013; Harsch *et al.*, 2014) with climate-sensitive (Chuine & Beaubien, 2001; Crozier & Dwyer, 2006) and dispersal (Iverson *et al.*, 2011) processes are under-utilized compared to traditional correlative climate niche models (Franklin, 2010; Dormann *et al.*, 2012). Until recently, range-shift models have not explicitly considered constraints on early life history stages (Jackson *et al.*, 2009) (but see (Conlisk *et al.*, 2017a)), climate-dependent vital rates (but see (Fordham *et al.*, 2013) and closely related process-based models (Morin & Thuiller, 2009; Coops & Waring, 2011)), or ecotype-dependent vital rates. Climate niche modeling results suggest that population-level genetic variation can greatly expand the total amount of climate space suitable to a species because the sum of many niche models fit to multiple 'population centers' tends to be markedly larger than the individual niche of any single population center (Benito Garzón *et al.*, 2011). Adding provenance-based recruitment differences to demographic models may enable evolving ecotypic variation that leads to greater species' abundance. To parameterize such models, data are needed on long-term demographic observations of adult trees and from *in situ* experiments focused on distributional shifts, a rarity in the ecological literature (Urban *et al.*, 2016).

Lodegpole pine is of particular interest because it is a common constituent of high-elevation forests in Western North America, with highly plastic responses to environmental conditions. Recruiting vigorously after fire, lodgepole pine can occur in monotypic stands

following recent fire disturbances or in mixed conifer forests with longer fire return intervals (>300 years). In stands with longer fire return intervals, lodgepole pine is typically replaced over time by more shade-tolerant species such as Engelmann spruce (*Picea engelmannii*) or subalpine fir (*Abies lasiocarpa*) (Despain, 1983; Lotan & Perry, 1983; Veblen, 1986; Sibold *et al.*, 2006; Pierce & Taylor, 2011). Longer fire return intervals typically occur at higher elevations where lodgepole pine has been shown to have lower overall serotiny compared to low elevations with frequent fires (Schoennagel *et al.*, 2003). Despite the importance of serotiny as a reproductive strategy, serotiny is heterogeneous across the landscape, due to a variety of factors including seed predation (Talluto & Benkman, 2014), and lodgepole pine can regenerate in the absence of fire (Lubetkin *et al.* In Press; Despain, 1983; Aoki *et al.*, 2011; Diskin *et al.*, 2011). With increasing fire predicted throughout Western North American forests below 2900m (Westerling, 2016) and post-fire lodgepole pine recruitment failure at many xeric sites (Donato *et al.*, 2016), shifting to higher elevations may be important to long-term lodgepole pine persistence in some areas, perhaps at the expense of less fire-adapted species. Lodgepole pine is currently not abundant at treeline in Colorado, where climate change is occurring more rapidly than the typical fire return interval. A better understanding of the conditions under which lodgepole pine can shift to higher elevations, in the presence and absence of fire, is critical to understanding long-term lodgepole pine demographics and distributions.

Here we report results from a novel field experiment designed to quantify the effects of heating on lodgepole pine (*Pinus contorta* Douglas var. latifolia) seedling recruitment in lower subalpine forest, where lodgepole pine currently occurs in a mixed conifer forest, and at treeline and alpine sites, where lodgepole pine is currently absent. Because heating can reduce soil moisture, we crossed a heating treatment with watering during the growing season to differentiate effects of heating from effects of soil drying. To test for effects of local

adaptation, we used common gardens sown with seeds collected locally from high and low elevations. We paired our experimental results with 35 years of demographic observations in the same forests to model effects of ecotypic differences and heating-induced changes in recruitment on tree populations using a stochastic, spatially explicit, demographic model. Using our data and models, we test: (i) whether heating reduces lodgepole pine recruitment in lower subalpine forest but promotes recruitment at and above treeline, where it does not currently occur, (ii) whether lodgepole pine seeds from low- or high- elevation provenances are better suited to colonize treeline and alpine sites under heating, (iii) the importance of the trade-off between dispersal distance and recruitment rates for modeled populations, and (iv) the relative rate of treeline and alpine colonization across different climate scenarios in the presence and absence of a fire disturbance. Our expectations are guided by previous work on Engelmann spruce and limber pine (*Pinus flexilis*) that showed decreased first-year recruitment with heating (Kueppers *et al.*, 2017), greater recruitment by low-elevation provenances even at and above treeline (Kueppers *et al.*, 2017), and transient, sometimes permanent, range contractions in modeled populations using observed climate-dependent changes to recruitment (Conlisk *et al.*, 2017a); however, these previous studies did not model the importance of seed provenance to demographics and range shifts.

Materials and methods

Experimental sites and treatments. Beginning in 2010, we established lodgepole pine (*Pinus contorta* Douglas var. latifolia) common garden experiments at three sites along an elevational gradient at Niwot Ridge in the Colorado Front Range, on the eastern slope of the Rocky Mountains (Castanha *et al.*, 2012): (i) a mature subalpine forest containing a mixture of lodgepole pine, Engelmann spruce (*Picea engelmannii* Parry ex. Engelm), subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall) and limber pine (*Pinus flexilis*), with little herb cover,

and near the lower elevation (3,060 m), "warm edge" of mixed subalpine forest and in the midst of lodgepole pine's elevation range, (ii) an open meadow surrounded by krummholz mats and low-tree islands near the climatically "cool edge" of subalpine forest (3,430 m), and (iii) an alpine meadow approximately 400 meters above timberline at 3,540 m (Figure 1). Lodgepole pine was a major constituent in the forest site, but was not present at the treeline and alpine sites. Mean annual air temperatures were 6.5±0.5, 7.1±0.5, and 9.8±0.4 °C for alpine, treeline, and forest sites, respectively, with snow-free growing season lengths of 140, 133, and 157 days (Table 1). Each site had 20 3-meter diameter plots assigned to one of four groups: control, heated, watered, and heated and watered (Figure 1). Plots were primarily SE-facing, spanning 79-194° across all sites with shallow slopes spanning 4-16°. Six 1000W Mor™ ceramic infrared heaters were arrayed around the perimeter of heated plots, following the geometry of Kimball *et al.* (2008). Active infrared heaters have significant methodological advantages, including nighttime heating and the ability to modify snowmelt timing (Aronson & McNulty, 2009), but do not typically affect air temperature and therefore relative humidity. Heater output was set to a constant 40% of maximum wattage (estimated 170 W/m^2 incident on the plots under low-wind conditions) in all sites during spring and summer months. Heaters were turned down to 10% (~40 W/m^2) during the windiest period of the year – mid November to early March – to avoid hydrological artifacts and intermittent snowpack (Meromy *et al.*, 2015). We raised and lowered heater scaffolding in alpine and treeline sites to keep heaters above the snow, repositioning them after snowmelt. We designed the watering treatments (2.5 mm/week) to compensate for the evaporative losses due to heating (determined at the start of the project from observed differences in the rate of forest soil drying at different temperatures), adding water manually once per week starting 2-3 weeks after snowmelt and ending in September. The added water, which was melted snow or locally pumped groundwater, amounted to a maximum of ~5% (~43 mm added) of the

long-term average annual

total precipitation at the sites (808 mm; Moyes *et al.*, 2015). Less water was added to treeline

plots and to unheated plots, which melted weeks later than other plots.

All plots were divided into four 1x1 m quadrants (Figure 1). To document

microclimate conditions, we placed one soil moisture and temperature sensor (ECTM or

5TM, Decagon Devices) at 5-10cm depth in the center of each quadrant (4 per plot) and

wired them to multiplexers and CR1000 dataloggers (Campbell Scientific). During the snow-

free periods of 2011-2015 (the period of this study), mean daily soil temperature was greater

in heated than unheated plots, with larger differences (3.9 °C) in the forest than in the alpine

(1.2 °C) because of higher wind speed at the alpine site (Table 1). At the treeline site, soil

temperature increase due to heating was similar to the alpine site (1.4 °C) in 2011-2014. In

2015, many heaters at the treeline site failed; thus, 2015 is excluded from statistical analysis

of heating effects. Heating alone tended to reduce soil moisture slightly, even in the alpine

and at treeline (Table 1). Finally, heating advanced the timing of snowmelt in all years and all

sites with the exception of the treeline site in 2011. The shortest snow-free seasons were

observed in 2011 and 2013. Watering did not significantly alter the plot temperature range,

but slightly increased soil moisture in all sites (Table 1).

Seedling observations. We collected lodgepole pine seeds from high-elevation (3070-

3300 m) and low-elevation (2630-2930 m) locations within 3 km of the experimental sites.

The 2011 cohort (defined as the year in which the seeds germinated) consisted only of low-

provenance seeds which were collected in the spring and stratified for 8 weeks prior to

sowing after snowmelt. Seeds for the 2012-2014 cohorts were collected in fall and sown prior

to snowfall, during the October-November. The lodgepole pine seeds were assigned to

twenty-four 10x10cm cells crisscrossing each quadrant. Low provenance seed was assigned

to quadrants containing Engelmann spruce in the remaining 70 cells while high provenance

seed was assigned to quadrants containing limber pine in the remaining 70 cells (Figure 1). We sowed 80-480 lodgepole pine seeds, buried at 1 cm depth, of each cohort per quadrant (a total of 245,000 seeds over 4 cohorts), making an effort to adjust the amount of seed according to viability as determined by x-ray (conducted by the USFS nursery in Coeur D'Alene, ID) and ensure adequate sample sizes. The lower limit on our seed densities is comparable to those seen in nature (Lotan & Perry, 1983). To exclude small granivorous mammals, we placed hardware cloth exclosures over each quadrant.

We tracked the number of seeds sown and number of seedlings surviving to autumn of each year in each cell. We quantified the fraction of seedlings surviving from seed to the autumn of their first year (first-year recruitment), from the autumn of their first year to autumn of their second year (second-year survival), from autumn of their second year to autumn of their third year (third-year survival), and from seed to three years (third-year recruitment). Because new seeds were sown each year (yielding 2011-2014 cohorts), we have the most observations for first-year recruitment (840 observations – with only low-provenance seeds for the 2011 cohort). For second-year survival, if all quadrants had at least one survivor, we would have 800 observations (from seedlings emerging in 2011-2014). Instead we obtained 490 observations because some quadrants had no individuals surviving their first year and 10 heated plots (40 quadrants) in the treeline site were excluded from the 2014 cohort due to heater failure (Table SI2.1 shows sample size across cohorts).

Statistical analysis. We estimated the effects of multiple factors on lodgepole pine seedling survival using a generalized linear mixed model (with plot and observation level random effects) with a logit link and binomial distribution in the R programming language (Bates *et al.*, 2015; R Core Team, 2017). Significance levels were estimated using likelihood ratio tests. Because GLMM likelihood ratio tests in R (lme4::glmer) do not automatically compute a likelihood ratio for main effects separately from their interactions, we directly

manipulated the design matrix (stats::model.matrix) to test main effects. In manipulating the design matrix, we chose sum contrasts (using "contr.sum" in R), where model intercepts are the average recruitment (or survival) across all factors and coefficient estimates are the deviation from this average for a given treatment. Thus, contrary to the default output in lme4::glmer, all levels across a factor should sum to zero (where there are two levels, we present just one because the other is the same magnitude but opposite sign).

Using a hypothesis-testing framework, which is consistent with a manipulation experiment, we considered main effects (heating, watering, provenance, site, and cohort) and all two-way interactions for first-year recruitment and only main effects for second- and third-year survival and third-year recruitment. We analyzed two subsets of the data: (1) the years in which there is a fully balanced treatment design (cohorts 2012-2014) and (2) all the data taken together, including the 2011 cohort which only had low-provenance seedlings and the 2015 data (in which heated treatments at the treeline site are not included due to heater failure). The first-year recruitment results for the former subset are included in the text, and results for the latter subset are placed in Supporting Information SI1 and are not qualitatively different. Third-year recruitment results for both subsets are presented below and annual second- and third-year survival for both subsets of data are placed in Supporting Information SI1.

Population model. To determine the influence on tree populations of observed seedling responses to climate treatments, we constructed a spatially-explicit, stochastic demographic model using RAMAS 5.0 (Akcakaya & Root, 2005). The RAMAS software allows for matrix, meta-population modeling with environmental stochasticity (vital rates change through time to incorporate changing environmental conditions) and demographic stochasticity (individuals have variable vital rates).

We assumed an annual time step and a three-patch meta-population, where the three

patches are analogous to our three experimental sites: a mature forest, and treeline and alpine

patches with initially no lodgepole pine individuals. We parameterized the first three life

stages using survival data from the experiment (Table S2.1). For these stages, individuals in

the model population either died or transitioned to a later life stage. At later life stages,

individuals died, remained in the same life stage, or transitioned to a later life stage.

Individuals could progress through the seedling and sapling stages (which we define as

individuals that have passed through seedling stages but have dbh<1cm) to become

reproductive adults in as few as 5 years, with an average age at first reproduction of about 14

years. Matrix transition rates for the 9 sapling stages were guided by literature values (Ying,

1991) (Supporting Information SI2). Values for adult transition rates were guided by

demographic data collected in long-term plots spanning 2980-3260 m at Niwot Ridge, CO

(Smith *et al.*, 2015). We derived survival for each adult stage as a function of measured

diameter at breast height for each individual in the plots (Supporting Information SI2). Using

data from younger stands (at elevations of 3020-3100 m), we assigned higher survival to

treeline and alpine plots because of the observed benefit of open canopies to early succession

lodgepole pine (Vander Wall, 2008). Additionally, individuals in treeline and alpine patches

had higher transition rates than individuals in forest sites because of the open canopies in

treeline and alpine patches. The average transit time to the largest stage was 235 years in

treeline and alpine sites and 320 years for the forest site. We may be over-estimating

population growth rates in modeled treeline and alpine patches because we used parameters

for tree growth rates and seed production derived from more favorable, lower elevation sites.

In total, we considered 16 models: four climate scenarios x two provenances x two fire

scenarios. In the four climate scenarios, which are analogous to our experimental treatment

groups (control, heated, watered, heated + watered), we parameterized seedling survival rates

using observations from our experiment. All other non-seedling vital rates were held constant

across the climate scenarios. In models with heating, we phased in the impacts of heating, transitioning linearly from unheated to heated rates over the first 100 years. For each of the climate scenarios, we considered models in which the forest patch occurred at 3330 m (high-provenance models) and 2970 m (low-provenance models), consistent with where seeds were collected for our common gardens. By changing only the seedling survival rates, these models were designed to assess how climate-driven changes and provenance differences in seedling survival affected the abundance of lodgepole pine and its expansion upward in elevation.

Because lodgepole pine is an early succession species, often regenerating after fire, we considered a forest in which there was no fire and one in which there was a fire 50 years after the start of the simulation. We only considered a single fire, early in the model time horizon because of the potential for post-fire recruitment to change dramatically over the next century, as temperatures rise. Time since last fire is spatially heterogeneous in the Colorado Front Range, with roughly 25% of forests with stands >400 years old (Sibold *et al.*, 2006). In the no-fire scenario, we set sapling and fecundity parameters (the most uncertain parameter values) such that the overall population growth rate for the control-climate, no-fire scenario was consistent with population growth rates from our long-term forest demography plots, or 0.995. This low growth rate is consistent with older, late seral stands, where fire occurred between 255-375 years prior, and where lodgepole pine is being replaced by Engelmann spruce and subalpine fir. In the fire scenario, we (i) increased forest seed supply, consistent with the release of seeds from serotinous cones (Crossley, 1956), (ii) increased first-year seedling survival rates, consistent with increased seedling survival in open canopies (Vander Wall, 2008), and (iii) increased survival and transition rates of lodgepole pine saplings to the rates in treeline and alpine patches (Supporting Information SI2). In models with fire, the climate scenarios were imposed on the treeline and alpine patches only. We parameterized

the forest patch with seedling survival rates from our control treatment only because we have no data on the combined impacts of fire and altered climate on seedling survival. While there are many uncertainties in the parameterization of the fire model, the goal was to consider a hypothetical forest with a growing population to serve as a vigorous propagule source for treeline and alpine populations. The fire scenarios could then be compared to the no-fire scenarios with declining forest populations.

Dispersal. We assume that uphill dispersal of lodgepole pine is possible and construct model scenarios to explore the trade-off between dispersal distance and varying survival across our two seed provenances. Each of the three patches was defined as an elevational band of 1 km^2 to ensure a model robust to demographic stochasticity. We parameterized our dispersal scenarios to compare the relative importance of high- versus low-provenance seeds in promoting colonization from the initially occupied forest patch to the initially unoccupied treeline and alpine sites. In the low-provenance model, the forest patch was assumed to occur 460 meters lower in elevation than the treeline patch (consistent with the highest elevation sites where low-provenance seeds were collected). In the high-provenance seed model, the forest patch was assumed to occur 100 meters below the treeline patch (consistent with the highest elevation sites where high-provenance seeds were collected). In both the high- and low-provenance seed models we assumed that treeline sites were 110 meters lower in elevation than alpine sites. We considered different mountain incline angles to consider a variety of potential dispersal distances and associated dispersal rates (see Table S1.3 for fractions of seed dispersing). Unless otherwise stated, the results show mountain incline angles of 20°. To parameterize dispersal rates, we chose a long-tail dispersal kernel (Clark *et al.*, 1999) fit to sparse dispersal data (Lotan & Perry, 1983). Supporting Information SI2 elaborates on model structure and parameter choice.

Results

Experimental treatments. For the 2012-2014 cohorts, first-year recruitment was lower in the forest (0.96%) compared to treeline (5.7%) and alpine (5.5%) sites. Heating decreased first-year recruitment by 44%, reducing cumulative germination and survival from 5.2% to 2.9% across sites (Table 2). Watering increased first-year recruitment by 31% (from 3.5% to 4.6% across sites). As expected, the negative effects of heating varied by site (Figure 2), with the most dramatic decrease in first-year recruitment (98.3%) in the forest. However, contrary to the expectation that heating would increase recruitment at the alpine and treeline sites, heating decreased first-year recruitment by 37.1% at the alpine site and by 38.2% at the treeline site. Contrary to the expectation of local adaptation, seeds from low-elevation seed provenances had greater recruitment across all sites (Table 2, Figure 2), with 2.0% recruitment for high- versus 6.0% for low-provenance seeds and no significant site by provenance interaction. The two provenances were similarly affected by heating and watering (Figure 2, Table 2).

The benefit of low-provenance seed varied significantly across cohorts. In 2012, low- and high-provenance seeds had nearly identical first-year recruitment (0.88% and 0.87% for high and low provenances, respectively), whereas in 2013 and 2014, first-year recruitment of low-provenance seeds was more than triple that of high (7.5% vs 2.2% in 2013 and 9.7% vs 3.0% in 2014). There was also significant variation across years, with the 2012 cohort having very low (0.9%) overall recruitment as compared to 4.8-6.4% in other years, and the alpine site having particularly low survival in 2012 (0.50% as compared to 6.0 and 9.9% in 2013 and 2014, leading to a significant site by year interaction). Lower survival in 2012 could be attributed to a very long and dry growing season and may explain that year's similar low- and high-provenance recruitment. In 2012, season lengths were 190, 154, and 180 days for forest,

treeline and alpine sites, respectively, and vapor pressure deficit was 0.70, 0.61, and 0.54 kPa (compare to Table 1).

Annual survival rates increased and became less sensitive to experimental treatments with seedling age (Supporting Information SI1). First-to-second year survival was 41.2% overall and second-to-third year survival was 71.0%. While heated plots had greater first-to-second year survival (47.5% heated vs 37.5% unheated) and second-to-third year survival (76.8% vs 68.2%), the effect of heating was not statistically significant (Tables SI1.2 and SI1.3). Watering resulted in a statistically significant increase in first-to-second year survival (44.4% watered vs 37.6% unwatered) and a non-significant increase in second-to-third year survival (73.7% vs 67.8%). Low-provenance seed had significantly greater first-to-second year survival across 2012-2014 (45.2% versus 40.4%) than high-provenance seed, but there was no significant provenance effect on second-to-third year survival (66.3% versus 73.6%).

Considering cumulative recruitment from seed to the third year (Figure 3, Table 3) for the 2011-2013 cohorts, heating significantly reduced recruitment (by 49%), watering significantly increased recruitment (by 108%), and low-provenance seeds had significantly greater recruitment (by 323%) than high-provenance seeds. Overall, recruitment to the first year largely determined the relative differences in recruitment across treatments (in other words, lines do not typically cross one another in Figure 3). When only the 2012 cohort is considered, in which high first-year mortality was observed for all sites and treatments, there are not enough observations to see an effect of watering and provenance, although a marginal heating effect is observed (Table 3, bottom half). For both subsets of data, there was a significant effect of site, with the highest survival in the treeline site.

Population model. Differences in seedling survival across climate treatments and between seed provenances resulted in very different modeled tree abundances across patches. In the no-fire models, populations declined in the forest across all scenarios, and most

dramatically for the heated and high-provenance scenarios (Figure 4). For the watered

scenarios for both provenances, mature (>4 cm dbh) treeline populations emerged after 300-

450 years, with more rapid population establishment for the high-provenance scenarios

because of a shorter assumed

dispersal distance between the forest and treeline patches. For the control scenario at treeline,

there was considerable population growth in the high-provenance but not the low-provenance

models. No treeline populations emerged under heating. In watered scenarios, alpine

colonization occurred in both low- and high-provenance scenarios 50-100 years after the

treeline populations began to emerge, with higher abundances in the high-provenance

scenarios.

For realistic mountain slope angles (as in Figure 4), both low- and high-provenance

seed sources are likely to contribute to population growth in treeline and alpine patches.

However, if the incline is steeper, creating shorter dispersal distances and higher fractions of

low-provenance seed moving upslope, larger populations emerge in the low-provenance

scenarios than in the high-provenance scenarios. For the combined heating and watering

scenario, across incline angles, it takes longer for the low provenance to reach a total

abundance of 750 mature trees in the alpine than for the high-provenance to reach the same

abundance (Figure 5). However, because of the relatively greater recruitment and survival of

low-provenance seeds, it takes the low provenance less time to grow from 750 to 20,000

individuals (Figure 5).

After fire, modeled high-provenance populations of lodgepole pine never recover to

pre-fire abundances, whereas, low-provenance populations recover from a fire after about

100 years, slightly exceeding their pre-fire abundances by 130 years post-fire (Figure 6).

With fire, the relative rankings of the climate scenarios at treeline and alpine sites are stable,

with the one exception being that the watering scenario has the greatest alpine abundance in

the low-provenance fire scenario while the heating and watering scenario has the greatest alpine abundance in the low-provenance no-fire scenario. With more robust forest populations, there is more rapid population growth in the treeline and alpine patches. There are also considerably larger populations in the low-provenance scenarios, suggesting that the greater survival of low-provenance seedlings observed in the experiment allows for more rapid population response to disturbance. Results are robust to sensitivity tests on vital rates (see Supporting Information SI3).

Discussion

Using active infrared heaters to explore the impact of climatic change on establishing seedlings within and beyond the elevation range of lodgepole pine, we found that heating reduced recruitment, especially in the lower elevation, mixed subalpine forest. Watering alleviated some of the negative effects of heating on recruitment, and in the absence of heating, increased recruitment. Our demographic models show that these observed changes in lodgepole pine recruitment were large enough to alter the trajectory of current forest populations and the pace of population establishment at higher elevations, consistent with previous work on limber pine and Engelmann spruce (Conlisk *et al.*, 2017a). Because of recruitment and dispersal-distance differences between low- and high-elevation seed provenances, seed origin was also important in dictating the rate of population emergence in the alpine. For the most rapid scenario of alpine colonization (under heating and watering), the emergence of small populations (approximately 750 trees) in the alpine occurred sooner with seed from a nearer, high-elevation patch. However, the emergence of large populations (approximately 20,000 trees) occurred more rapidly with seed from a more distant, low-elevation patch, because higher recruitment rates of low-provenance seeds overwhelmed longer dispersal distances. Despite much lower treeline abundances for the low- compared to

the high-provenance scenario, there were still enough individuals at treeline to facilitate alpine colonization. Thus, the treeline population under the low-provenance scenario can be thought of as a more "efficient" propagule source on a per tree basis. Regardless of seed origin, our model scenarios show considerable lags in establishment of mature trees in the alpine, consistent with previous models (Dullinger *et al.*, 2012; Conlisk *et al.*, 2017a). Long lags in climate warming-driven forest range shifts are consistent with empirical studies finding that tree establishment is not keeping pace with climate change (Sittaro *et al.*, 2017).

Population growth at treeline and beyond is based on our model parameterization which assumed sapling survival and adult transition rates from studies at lower elevations and an assumed extra benefit of open canopy conditions. Such high sapling and adult growth rates at treeline and alpine sites likely overestimate lodgepole pine colonization beyond their current elevation range. Our scenarios may also underestimate the negative impacts of warming because we assumed no further climate change after the first 100 years and limited heating (increase of approximately ~1.5° C) at the treeline and in the alpine. Models that included fire are particularly uncertain because the combined effect of heating and disturbance on recruitment is unknown. Because larger, post-fire forest abundances provided enough propagules to facilitate dispersal to higher elevations, modeled colonization to treeline and alpine sites under warming was much higher in models with fire as compared to models with no fire. However, the forest populations in fire models were parameterized using the higher recruitment rates seen in the control treatment of our experiment, whereas recent studies show recruitment failure under warmer, drier conditions (Donato *et al.*, 2016). To determine the potential for future lodgepole pine range shifts, field research is necessary focusing on the interaction between heating and disturbance. Regardless of whether we have over- or underestimated the long-term population growth rate of lodgepole pine, our sensitivity tests demonstrate that the relative rankings of climate scenarios and modeled lags

in alpine colonization are robust to changes in population growth rates.

At the low-elevation, warm edge of mixed subalpine forest, heating caused more dramatic declines in first-year recruitment compared to the other sites, as it did for other subalpine species (Kueppers *et al.*, 2017). While we expected low lodgepole pine recruitment in our mature forest site, decreased recruitment due to heating could have occurred because seedlings were already near a thermal limit or because of higher realized experimental heating (4℃ increase in heated forest plots versus <2℃ in treeline and alpine plots). Other studies have found lodgepole pine germination to be heat-sensitive (Kaufmann & Eckard, 1977; Petrie *et al.*, 2016). Recent studies of post-fire recruitment show recruitment failure at some dry sites (Donato *et al.*, 2016), consistent with our results showing moisture sensitivity. Warming at low elevations may also be detrimental to older life stages. Adult mortality of limber pine, Engelmann spruce, and lodgepole pine appears to have increased with warming from 1982-2013 (Smith *et al.*, 2015). Adult lodgepole pine growth has also been shown to decline with high temperatures in the current and previous summer growing seasons (Villalba *et al.*, 1994; Chhin *et al.*, 2008), due, in part, to increases in moisture stress.

Comparing lodgepole pine, which currently occurs in lower elevation, warmer stands at our site, to Engelmann spruce and limber pine, which currently occur at treeline, it is not clear which species, if any, is more likely to advance treeline. In the absence of fire, lodgepole pine's negative response to *in situ* heating combined with adult demographics from declining forest stands led to a decrease in modeled propagules colonizing new habitat, suggesting that lodgepole pine is unlikely to "leapfrog" existing treeline species. However, in the presence of fire, there was considerably more alpine colonization with heating and watering, especially for low-provenance seed, making it theoretically possible for lodgepole pine to "leapfrog" existing treeline species to become a significant alpine colonist. In the same plots, Engelmann spruce showed recruitment declines similar to lodgepole pine with

heating (Kueppers *et al.*, 2017). Limber pine showed initially lower first-year recruitment with heating, which was offset in later years yielding similar recruitment to the fourth year in heated and unheated plots. In models, both Engelmann spruce and limber pine showed considerable lags in alpine colonization, with longer lags and potentially permanent range contraction for Engelmann spruce (Conlisk *et al.*, 2017a). Although lodgepole pine and Engelmann spruce are currently more abundant at our site, limber pine's reduced sensitivity to heating may make it a larger component of future forests, shifting Rocky Mountain species composition. Regardless, recruitment of limber pine, Engelmann spruce, and lodgepole pine did not benefit from warming when compared to recruitment observed in the absence of warming. Other studies have shown that non-treeline species sown at or above treeline in the absence of warming can do well (Bansal & Germino, 2008; Fajardo & Piper, 2014). Reductions in seedling establishment above treeline and consequent reductions in population growth rates with warming suggest that upslope shifts in the position of treeline may slow or stall in the future, consistent with a global meta-analysis showing that treeline elevation has remained constant with 20th Century warming in about half of the sites surveyed (Harsch *et al.*, 2009).

Physiological performance during the seedling stage is under strong natural selection, as attested by decades of forestry research into increasing outplanting success via genetic screening and breeding (known as "tree improvement" programs) and seed and seedling pre-treatments (Burdett, 1983; Ritchie *et al.*, 1985). Combining provenance studies and climate modeling, (Wang *et al.*, 2006) concluded that the pace of climate change may necessitate a rethinking of seed deployment strategies. They found that productivity and populations of lodgepole pine could be enhanced by facilitating migration of provenances over greater distances than is currently done under the "local is best" mindset (Aitken & Bemmels, 2016). We found no evidence for local adaptation of lodgepole pine at the seedling establishment

phase and both provenances had a similar response to heating (there was not a significant site by heating interaction). It is not clear why low-elevation seeds experienced superior survival. High-elevation seeds were not consistently smaller or less viable than low-elevation seeds, suggesting that maternal provisioning of low-elevation seeds does not obviously explain increased recruitment. Low-provenance lodgepole pine seedlings were observed to emerge earlier across sites (unpublished data), a trait that could have afforded low-provenance seedlings a recruitment advantage. Lack of local adaptation may be a sign that lodgepole seedlings are already at disequilibrium with 20th Century warming, with current treeline and alpine sites more climatically similar to lower elevation sites of the past.

Regardless, our results agree with the hypothesis that lower elevation populations and even the "trailing edge" of species ranges will be important in facilitating species persistence (Hampe & Petit, 2005). Because of the higher survival of the more distant, low provenance seeds, we found that there was a trade-off between dispersal distance and survival, where slopes with incline angles steeper than 20° were likely to have populations dominated by low-elevation propagules. Thus, low-elevation lodgepole pine propagules could "leapfrog" populations of high-elevation genotypes to establish in warming treeline and alpine sites. Our results suggest that ignoring ecotypic variation may neglect important processes that drive how species respond to climate change across landscapes (Benito Garzón *et al.*, 2011).

To extend this work, a number of model assumptions could be revisited, including (i) obtaining and incorporating treeline-specific adult vital rates (instead we used forest survival rates as in (Smith, 2012)), (ii) obtaining and incorporating climate- and provenance-specific vital rates across non-seedling life stages, and (iii) obtaining and incorporating vital rates following fire and under climate manipulations. It is unlikely that adult lodgepole pines would have higher adult growth and survival rates at treeline than in the forest. Thus, our model, which had greater survival rates in the open canopy at treeline, likely led to an

overestimate of lodgepole pine abundances at treeline. Other studies have shown that different life stages can respond differently to climate (Doak & Morris, 2010; Villellas *et al.*, 2015) and ecotype can mediate the interaction between life stage and climate (Guy & Holowachuk, 2001). Future models should incorporate provenance-specificity and climate-dependence across life stages, allowing the potential for later life stages to overcome poor provenance- or climate-based recruitment in early life stages. Small shifts in more reproductively-active, later life stages are likely to be very important to lodgepole pine demographics, and shifts in adult survival have already been observed (van Mantgem *et al.*, 2009; McDowell & Allen, 2015). Finally, we assumed a post-fire forest regeneration scenario based on the parameterization from our control scenario due to a lack of data on the combined effects of warming and fire on recruitment. This parameterization allowed us to test whether increased seed availability due to the opening of serotinous cones (Alexander & Cruz, 2012; Buma *et al.*, 2013) and enhanced recruitment due to an open canopy (Vander Wall, 2008) altered the ranking of the different climate scenarios. However, with better data on post-fire recruitment under warming, future models could include these combined effects.

Our study focused exclusively on the direct effects of climate change and ignored the indirect effects of climate change on mountain pine beetle and fire frequency (Williams *et al.*, 2010). As a post-fire primary colonizer, lodgepole pine is likely to be affected by increases in fire frequency anticipated with climate change (Abatzoglou & Williams, 2016; Westerling, 2016). Mountain pine beetle outbreaks also have increased substantially over the past few decades due to climate change (Chapman *et al.*, 2012; Mitton & Ferrenberg, 2012), and are likely to continue to increase under future warming and drying (Bentz *et al.*, 2010). Thus, a full understanding of the trajectory of lodgepole pine populations under climate change should consider the suite of impacts from climate change.

In summary, we observed decreased lodgepoloe pine recruitment with heating across an elevation gradient, with no evidence of local adaptation. Low-provenance seeds recruited more strongly across the elevation gradient, but were as vulnerable to heating as high-provenance seeds. Using these observations in models of lodgepole pine populations demonstrated that greater recruitment of low-provenance seeds was sufficient to overcome longer dispersal distances for treeline and alpine colonization, assuming long (multi-century) timescales. On shorter timescales, small populations emerged from more proximal maladapted ecotypes, but these populations did not grow as rapidly as those from more distant, well-adapted ecotypes. While recruitment rates were low overall, the establishment of lodgepole pine above its current elevation range combined with enhanced recruitment from ecotypes from lower elevations suggest that propagules from the lower, warmer portions of species' ranges could drive upslope range shifts with climate change.

References

Abatzoglou JT, Williams AP (2016) Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences*, **113**, 11770–11775.

Aitken SN, Bemmels JB (2016) Time to get moving: assisted gene flow of forest trees. *Evolutionary Applications*, **9**, 271–290.

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, **1**, 95–111.

Akcakaya HR, Root W (2005) *RAMAS GIS: Viability Analysis for Stage-structured metapopulations (Version 5).* Applied Biomathematics, Setauket, New York.

Alberto FJ, Aitken SN, Alía R et al. (2013) Potential for evolutionary responses to climate change – evidence from tree populations. *Global Change Biology*, **19**, 1645–1661.

Alexander ME, Cruz MG (2012) Modelling the effects of surface and crown fire behaviour on serotinous cone opening in jack pine and lodgepole pine forests. *International Journal of Wildland Fire*, **21**, 709–721.

Allen CD, Macalady AK, Chenchouni H et al. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.

Aoki CF, Romme WH, Rocca ME (2011) Lodgepole Pine Seed Germination Following Tree Death from Mountain Pine Beetle Attack in Colorado, USA. *The American Midland Naturalist*, **165**, 446–451.

Aronson EL, McNulty SG (2009) Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology*, **149**, 1791–1799.

Bansal S, Germino MJ (2008) Carbon Balance of Conifer Seedlings at Timberline: Relative Changes in Uptake, Storage, and Utilization. *Oecologia*, **158**, 217–227.

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using {lme4}. *Journal of Statistical Software*, **67**, 1–48.

Benito Garzón M, Alía R, Robson TM, Zavala MA (2011) Intra-specific variability and plasticity influence potential tree species distributions under climate change. *Global Ecology and Biogeography*, **20**, 766–778.

Bentz BJ, Régnière J, Fettig CJ et al. (2010) Climate Change and Bark Beetles of the Western United States and Canada: Direct and Indirect Effects. *BioScience*, **60**, 602–613.

Buma B, Brown CD, Donato DC, Fontaine JB, Johnstone JF (2013) The Impacts of Changing Disturbance Regimes on Serotinous Plant Populations and Communities. *BioScience*, **63**, 866–876.

Burdett AN (1983) Quality control in the production of forest planting stock. *Forestry Chronicle*, **59**, 132–138.

Castanha C, Torn MS, Germino MJ, Weibel B, Kueppers LM (2012) Conifer seedling recruitment across a gradient from forest to alpine tundra: effects of species, provenance, and site. *Plant Ecology & Diversity*, **6**, 307–318.

Chapman TB, Veblen TT, Schoennagel T (2012) Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology*, **93**, 2175–2185.

Chhin S, Hogg EH (Ted), Lieffers VJ, Huang S (2008) Potential effects of climate change on the growth of lodgepole pine across diameter size classes and ecological regions. *Forest Ecology and Management*, **256**, 1692–1703.

Chuine I, Beaubien EG (2001) Phenology is a major determinant of tree species range. *Ecology Letters*, **4**, 500–510.

Clark JS, Silman M, Kern R, Macklin E, HilleRisLambers J (1999) Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, **80**, 1475–1494.

Conlisk E, Syphard AD, Franklin J, Flint L, Flint A, Regan H (2013) Uncertainty in assessing the impacts of global change with coupled dynamic species distribution and population models. *Global Change Biology*, **19**, 858–869.

Conlisk E, Castanha C, Germino MJ, Veblen T, Smith JM, Kueppers LM (2017a) Declines in low-elevation subalpine tree populations outpace growth in high-elevation populations with warming. *Journal of Ecology*.

Conlisk E, Castanha C, Germino MJ, Veblen TT, Smith JM, Moyes AB, Kueppers LM (2017b) Data from: Seed origin and warming constrain lodgepole pine recruitment, slowing the pace of population range shifts. *Dryad Digital Repository*. https://doi:10.5061/dryad.tk1v8

Coops N, Waring R (2011) A process-based approach to estimate lodgepole pine (Pinus contorta Dougl.) distribution in the Pacific Northwest under climate change. *Climatic Change*, **105**, 313–328.

Crossley D (1956) Fruiting habits of lodgepole pine. *Forest Research Division Technical Note*, 1–32.

Crozier L, Dwyer G (2006) Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. *American Naturalist*, **167**, 853–866.

Dai A (2013) Increasing drought under global warming in observations and models. *Nature Clim. Change*, **3**, 52–58.

Davis MB, Shaw RG, Etterson JR (2005) Evolutionary responses to changing climate. *Ecology (Washington D C)*, **86**, 1704–1714.

Despain DG (1983) Nonpyrogenous Climax Lodgepole Pine Communities in Yellowstone National Park. *Ecology*, **64**, 231–234.

Diskin M, Rocca ME, Nelson KN, Aoki CF, Romme WH (2011) Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain National Park, Colorado. *Canadian Journal of Forest Research*, **41**, 782–792.

Doak DF, Morris WF (2010) Demographic compensation and tipping points in climate-induced range shifts. *Nature*, **467**, 959–962.

Donato DC, Harvey BJ, Turner MG (2016) Regeneration of montane forests 24 years after the 1988 Yellowstone fires: A fire-catalyzed shift in lower treelines? *Ecosphere*, **7**, e01410–n/a.

Dormann CF, Schymanski SJ, Cabral J et al. (2012) Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography*, **39**, 2119–2131.

Dullinger S, Gattringer A, Thuiller W et al. (2012) Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Clim. Change*, **2**, 619–622.

Dullinger S, Dendoncker N, Gattringer A et al. (2015) Modelling the effect of habitat fragmentation on climate-driven migration of European forest understorey plants. *Diversity and Distributions*, **21**, 1375–1387.

Fajardo A, Piper FI (2014) An experimental approach to explain the southern Andes elevational treeline. *American Journal of Botany*, **101**, 788–795.

Fordham DA, Mellin C, Russell BD et al. (2013) Population dynamics can be more important than physiological limits for determining range shifts under climate change. *Global Change Biology*, **19**, 3224–3237.

Franklin J (2010) Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, **16**, 321–330.

Guy RD, Holowachuk DL (2001) Population differences in stable carbon isotope ratio of Pinus contorta Dougl. ex Loud.: relationship to environment, climate of origin, and growth potential. *Canadian Journal of Botany*, **79**, 274–283.

Hampe A, Petit R (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461–467.

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.

Harsch MA, Zhou Y, HilleRisLambers J, Kot M (2014) Keeping Pace with Climate Change: Stage-Structured Moving-Habitat Models. *The American Naturalist*, **184**, 25–37.

Iverson LR, Prasad AM, Matthews SN, Peters MP (2011) Lessons Learned While Integrating Habitat, Dispersal, Disturbance, and Life-History Traits into Species Habitat Models Under Climate Change. *Ecosystems*, **14**, 1005–1020.

Jackson ST, Betancourt JL, Booth RK, Gray ST (2009) Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 19685–19692.

Jump AS, Hunt JM, Martinez-Izquierdo JA, Penuelas J (2006) Natural selection and climate change: temperature-linked spatial and temporal trends in gene frequency in Fagus sylvatica. *Molecular Ecology*, **15**, 3469–3480.

Kaufmann M, Eckard A (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.

Kueppers LM, Conlisk E, Castanha C et al. (2017) Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. *Global Change Biology*, **23**, 2383–2395.

Lotan JE, Perry DA (1983) *Ecology and regeneration of lodgepole pine*, Agriculture Handbook No. 606 edn. United States Department of Agriculture, Forest Service.

Lubetkin KC, Westerling AL, Kueppers LM Climate and landscape drive the pace and pattern of conifer encroachment into subalpine meadows. *Ecological Applications*, n/a-n/a.

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.

McDowell NG, Allen CD (2015) Darcy's law predicts widespread forest mortality under climate warming. *Nature Clim. 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.

Meromy L, Molotch NP, Williams MW, Musselman KN, Kueppers LM (2015) Snowpack-climate manipulation using infrared heaters in subalpine forests of the Southern Rocky Mountains, USA. *Agricultural and Forest Meteorology*, **203**, 142–157.

Mitton JB (1995) Genetics and the physiological ecology of conifers. In: *Ecophysiology of Coniferous Forests* (eds Smith WK, Hinckley TM), pp. 1–36. Academic Press, Inc., San Diego, CA USA.

Mitton JB, Duran KL (2004) Genetic variation in pinin pine, Pinus edulis associated with summer precipitation. *Molecular Ecology*, **13**, 1259–1264.

Mitton JB, Ferrenberg SM (2012) Mountain Pine Beetle Develops an Unprecedented Summer Generation in Response to Climate Warming. *American Naturalist*, **179**, E163–E171.

Morin X, Thuiller W (2009) Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology*, **90**, 1301–1313.

Mosca E, Eckert AJ, Di Pierro EA, Rocchini D, La Porta N, Belletti P, Neale DB (2012) The geographical and environmental determinants of genetic diversity for four alpine conifers of the European Alps. *Molecular Ecology*, **21**, 5530–5545.

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.

Petrie MD, Wildeman AM, Bradford JB, Hubbard RM, Lauenroth WK (2016) A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. *Forest Ecology and Management*, **361**, 328–338.

Pierce AD, Taylor AH (2011) Fire severity and seed source influence lodgepole pine (Pinus contorta var. murrayana) regeneration in the southern cascades, Lassen volcanic National Park, California. *Landscape Ecology*, **26**, 225–237.

R Core Team (2017) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rehfeldt GE, Ying CC, Spittlehouse DL, Hamilton DA (1999) Genetic responses to climate in Pinus contorta: niche breadth, climate change, and reforestation. *Ecological Monographs*, **69**, 375–407.

Reich PB, Oleksyn J (2008) Climate warming will reduce growth and survival of Scots pine except in the far north. *Ecology Letters*, **11**, 588–597.

Reich PB, Oleksyn J, Tjoelker MG (1996) Needle Respiration and Nitrogen Concentration in Scots Pine Populations from a Broad Latitudinal Range: A Common Garden Test with Field-Grown Trees. *Functional Ecology*, **10**, 768–776.

Ritchie GA, Roden JR, Kleyn NA (1985) Physiological quality of lodgepole pine and interior spruce seedlings: effects of lift date and duration of freezer storage. *Canadian Journal of Forest Research*, **15**, 636–645.

Savolainen O, Pyhajarvi T, Knurr T (2007) Gene flow and local adaptation in trees. *Annual Review of Ecology Evolution and Systematics*, **38**, 595–619.

Schoennagel T, Turner MG, Romme WH (2003) The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone National Park. *Ecology*, **84**, 2967–2978.

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.

Seager R, Ting M, Held I et al. (2007) Model Projections of an Imminent Transition to a More Arid Climate in Southwestern North America. *Science*, **316**, 1181.

Sibold JS, Veblen TT, González ME (2006) Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. *Journal of Biogeography*, **33**, 631–647.

Sittaro F, Paquette A, Messier C, Nock CA (2017) Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. *Global Change Biology*, n/a-n/a.

Smith JM (2012) An examination of background tree mortality and mountain pine beetle disturbance in subalpine forests of the Front Range of Colorado, USA. **Ph.D. dissertation**, **University of Colorado Boulder.**

Smith JM, Paritsis J, Veblen T, 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.

Talluto MV, Benkman CW (2014) Conflicting selection from fire and seed predation drives fine-scaled phenotypic variation in a widespread North American conifer. *Proceedings of the National Academy of Sciences*, **111**, 9543–9548.

Urban MC, Bocedi G, Hendry AP et al. (2016) Improving the forecast for biodiversity under climate change. *Science*, **353**.

Vander Wall SB (2008) On the relative contributions of wind vs. animals to seed dispersal of four Sierra Nevada pines. *Ecology*, **89**, 1837–1849.

Veblen TT (1986) Age and size structure of subalpine forests in the Colorado Front Range. *Bulletin of the Torrey Botanical Club*, **113**, 225–240.

Villalba R, Veblen TT, Ogden J (1994) Climatic Influences on the Growth of Subalpine Trees in the Colorado Front Range. *Ecology*, **75**, 1450–1462.

Villellas J, Doak DF, García MB, Morris WF (2015) Demographic compensation among populations: what is it, how does it arise and what are its implications? *Ecology Letters*, **18**, 1139–1152.

Wang T, Hamann A, Yanchuk A, O'Neill GA, Aitken SN (2006) Use of response functions in selecting lodgepole pine populations for future climates. *Global Change Biology*, **12**, 2404–2416.

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.

Westerling AL (2016) Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **371**.

Williams AP, Allen CD, Millar CI, Swetnam TW, Michaelsen J, Still CJ, Leavitt SW (2010) Forest responses to increasing aridity and warmth in the southwestern United States. *Proceedings of the National Academy of Sciences*, **107**, 21289–21294.

Williams AP, Allen CD, Macalady AK et al. (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Clim. Change*, **3**, 292–297.

Wu HX, Ying CC (2004) Geographic pattern of local optimality in natural populations of lodgepole pine. *Forest Ecology and Management*, **194**, 177–198.

Ying CC (1991) Performance of lodegpole pine provenances at sites in Southwestern British Columbia. *Silvae Genetics*, **40**, 215–223.

Supporting Information

SI1. Additional seedling survival results

SI2. Model parameterization.

SI3. Model sensitivity.

SI4. Models and model results are archived in the Dryad Digital Repository https://doi:10.5061/dryad.tk1v8 (Conlisk *et al.*, 2017b). Seedling recruitment data can be obtained by contacting the authors.

Tables

Table 1. Daily mean site climate, soil microclimate and treatment effects. Data for the top four rows come from meteorological stations at each site and data for the bottom eight rows come from soil temperature and moisture sensors averaged over plots at each site. Values encompass 2011-2015 measurements except where noted. Standard errors in parentheses are propagated across days from the average across plots. Abbreviations are photosynthetically active radiation (PAR); vapor pressure deficit (VPD); snow-free season length (SL; determined from diel variability in soil temperature); 5-10cm soil volumetric water content (VWC); heating effects on 5-10cm soil temperature (ΔT_H), snow-free season length (ΔSL_H), and volumetric water content (ΔVWC_H); and watering effect on 5-10cm soil volumetric water content (ΔVWC_W). Mean soil temperature, mean SL and mean soil VWC were calculated over the snow-free season from control plots only.

	Forest 3060 m	Treeline 3430 m	Alpine 3540 m
Mean Air Temp (°C)	9.8 (0.4)	7.1 (0.5)	6.5 (0.5)
PAR (mmol m^{-2} s^{-1})	175 (9)	434 (12)	432 (12)
Wind (m s^{-1})	0.2 (0.0)	3.6 (0.2)	5.6 (0.3)*
VPD (kPa)	0.65 (0.01)	0.52 (0.01)	0.47 (0.01)
Mean Soil Temp (°C)	9.2 (0.2)	9.3 (0.1)	8.5 (0.1)
Mean SL (days)	157 (9)	133 (8)	140 (10)
Mean Soil VWC,(m^3 m^{-3})	0.167 (0.008)	0.259 (0.006)	0.243 (0.007)
ΔT_H (°C)	3.87 (0.03)	1.37 (0.05)**	1.21 (0.03)
ΔSL_H (days)	31 (5)	10 (4)**	11 (3)
ΔVWC_H (m^3 m^{-3})	-0.006 (0.001)	-0.010 (0.001)**	-0.012 (0.001)
ΔVWC_W (m^3 m^{-3})	0.018 (0.000)	0.008 (0.001)**	0.012 (0.001)

* Wind speed values are unavailable from the alpine site in 2015.
** The heating treatment was not running in 2015 at Treeline, so the Treeline heating and watering effect calculations include only 2011-2014.

Table 2. Generalized linear mixed effects model parameter estimates, likelihood ratio tests (LRT), and P-values $P(\chi^2)$, for treatments, seed provenance, sites, cohorts and all two-way interactions on first-year recruitment for lodgepole pine seedlings emerging in 2012-2014. We show coefficients for all three sites but omit the coefficient for treatments with only two levels (i.e. Heat, Water, and Provenance) because the coefficient for the level not shown has the same magnitude but opposite sign as the coefficient shown (e.g. No Heat would be 0.90). Random effects variances are 0.17 for Plot and 0.61 for the observation level random effect. Intercept refers to the average log-odds for all levels. Cohort indicates the year that the seedling emerged. Probabilities <0.05 are given in bold type.

	Estimate	SE	LRT (df)	$P(\chi^2)$
Intercept	-4.79	0.09		
Heat	-0.90	0.09	75.38 (1)	**< 10^{-5}**
Water	0.21	0.08	7.36 (1)	**0.0067**
Provenance (Low)	0.38	0.05	54.75 (1)	**< 10^{-5}**
Site			137.26 (2)	**< 10^{-5}**
Site (Forest)	-2.34	0.16		
Site (Treeline)	1.39	0.11		
Site (Alpine)	0.95	0.11		
Cohort			253.84 (2)	**< 10^{-5}**
Cohort (2014)	0.78	0.07		
Cohort (2013)	0.61	0.07		
Cohort (2012)	-1.39	0.10		
Heat x Water	0.14	0.07	3.58 (1)	0.059
Heat x Provenance (Low)	-0.00	0.04	0.00 (1)	0.97
Heat x Site			55.93 (2)	**<10^{-5}**
Heat x Site (Forest)	-1.07	0.14		
Heat x Site (Treeline)	0.51	0.10		
Heat x Site (Alpine)	0.55	0.10		
Heat x Cohort			3.38 (2)	0.18
Heat x Cohort (2014)	0.09	0.06		
Heat x Cohort (2013)	-0.07	0.06		
Heat x Cohort (2012)	-0.03	0.08		
Water x Provenance (Low)	0.03	0.04	0.65 (1)	0.42
Water x Site			0.30 (2)	0.86
Water x Site (Forest)	0.02	0.12		
Water x Site (Treeline)	-0.05	0.10		
Water x Site (Alpine)	0.03	0.10		
Water x Cohort			1.07 (2)	0.59
Water x Cohort (2014)	0.06	0.06		
Water x Cohort (2013)	-0.01	0.06		

Water x Cohort (2012)	-0.04	0.07		
Provenance x Site			3.15 (2)	0.21
Provenance (Low) x Site (Forest)	-0.13	0.07		
Provenance (Low) x Site (Treeline)	0.05	0.06		
Provenance (Low) x Site (Alpine)	0.08	0.06		
Provenance x Cohort			36.48 (2)	**< 10^{-5}**
Provenance (Low) x Cohort (2014)	0.23	0.06		
Provenance (Low) x Cohort (2013)	0.23	0.06		
Provenance (Low) x Cohort (2012)	-0.45	0.07		
Site x Cohort			43.46 (4)	**< 10^{-5}**
Site (Forest) x Cohort (2014)	-0.15	0.12		
Site (Forest) x Cohort (2013)	0.13	0.12		
Site (Forest) x Cohort (2012)	0.03	0.18		
Site (Treeline) x Cohort (2014)	-0.27	0.08		
Site (Treeline) x Cohort (2013)	-0.19	0.08		
Site (Treeline) x Cohort (2012)	0.46	0.11		
Site (Alpine) x Cohort (2014)	0.42	0.09		
Site (Alpine) x Cohort (2013)	0.06	0.09		
Site (Alpine) x Cohort (2012)	-0.48	0.13		

Table 3. Generalized linear mixed effects model parameter estimates, likelihood ratio tests (LRT), and P-values $P(\chi^2)$, for main effects of treatment, seed provenance, site, and cohort on third-year recruitment for lodgepole pine seedlings emerging in 2011-2013 (upper half of table) and 2012 only (lower half of table), omitting the Forest site for the 2012 only analysis because there were no survivors. We omit the coefficient for main effects with only two levels because the coefficient for the level not shown has the same magnitude but opposite sign as the coefficient shown. Random effects variances are 0.85 for Plot and 1.08 for the observation level random effect for seedlings emerging in 2011-2013, and 0.41 and 0.66 for seedlings emerging in 2012. Intercept refers to the average log-odds for all levels (sum contrasts were used).

Seedlings emerging in 2011-2013	Estimate	SE	LRT (df)	$P(\chi^2)$
Intercept	-6.62	0.20		
Heat	-0.48	0.16	9.44 (1)	**0.0021**
Water	0.43	0.15	7.45 (1)	**0.0064**
Provenance (Low)	0.57	0.09	39.17 (1)	**$< 10^{-5}$**
Site			81.04 (2)	**$< 10^{-5}$**
Site (Forest)	-2.62	0.28		
Site (Treeline)	1.93	0.23		
Site (Alpine)	0.69	0.22		
Cohort			110.98 (2)	**$< 10^{-5}$**
Cohort (2013)	0.91	0.12		
Cohort (2012)	-1.19	0.13		
Cohort (2011)	0.27	0.13		
Seedlings emerging in 2012	Estimate	SE	LRT (df)	$P(\chi^2)$
Intercept	-6.71	0.33		
Heat	-0.40	0.21	3.56 (1)	0.059
Water	0.28	0.20	1.73 (1)	0.19
Provenance (Low)	0.04	0.15	0.08 (1)	0.78
Site (Treeline)	1.48	0.29	28.77 (1)	**$< 10^{-5}$**

Figure captions

Figure 1. Schematic of the Alpine Treeline Warming Experiment. Sixty plots were sown with high- and low-elevation lodgepole pine seed, interspersed with either limber pine or Engelmann spruce seedlings. The alpine site is above treeline at 3,540 meters. The treeline site is at 3,430 meters at the "cold edge" of subalpine forest. The forest site is in a mature forest at 3,060 meters near the "warm edge" of mixed subalpine forest (lodgepole pine range extends to lower elevations). At the center of each plot and each quadrant, soil temperature and moisture sensors recorded microclimate at a depth of 5-10 cm. Six infrared heaters were suspended 1.2 m above heated plots on scaffolding that was raised and lowered with the accumulation and melt of snow. Watered plots received 2.5 mm per week during the growing season.

Figure 2. Lodgepole pine first-year recruitment from 2011-2014 under experimental heating and watering for (a) high-provenance and (b) low-provenance seed at forest, treeline and alpine sites.

Figure 3. Lodgepole pine cumulative survival curves from 2011-2014 for experimental treatments at (a) alpine, (b) treeline, and (c) forest sites. Points are mean survival values calculated across the years for which data are available. Dashed lines are high-provenance and solid lines are low-provenance survival.

Figure 4. Abundance of high- (left column: a, c, e) and low- (right column: b, d, f) provenance mature trees (>4 cm diameter at breast height, dbh) through time for four climate scenarios under the no-fire scenario: control, heating (heat), watering (water), and heating plus watering (heat-water). Models included three patches: alpine (a, b), treeline (c, d), and

forest (e, f) that interacted through dispersal. Shaded areas delineate one standard deviation across 1000 model runs for each year. Vertical lines show when the heat-water scenario forest populations declined to 50% of their initial abundance (solid) and when the treeline heat-water scenario population grew to 50% of the initial forest abundance (dashed). The horizontal arrows show the lag between the decline in forest populations and emergence of treeline populations in the heat-water scenario. Incline angle was assumed to be 20°.

Figure 5. Time to reach 750 individuals (gray symbols) and 20,000 individuals (black symbols) in the alpine patch under the heat-water scenario for high-provenance (triangles) and low-provenance (squares) seeds as a function of the incline angle of the mountain. Steeper incline angles mean shorter modeled dispersal distances and thus more propagules moving from the forest to treeline and treeline to alpine patches.

Figure 6. Abundance of high- (left column: a, c, e) and low- (right column: b, d, f) provenance mature trees (>4 cm diameter at breast height, dbh) through time for four climate scenarios under the fire scenario: control, heating (heat), watering (water), and heating plus watering (heat-water). Models included three patches: alpine (a, b), treeline (c, d), and forest (e, f) that interacted through dispersal. Shaded areas delineate one standard deviation across 1000 model runs for each year. Because there was no data on the combined impact of fire and altered climate on seedling survival, we parameterized the forest model using seedling survival from our control treatment. Thus, each of the populations in the treeline and alpine patches were modeled assuming the same forest population. Incline angle was assumed to be 20°. The heat-watered scenario largely overlaps the watered scenario.

Alpine, 3540 m

Treeline, 3430 m

3 m

2 m

● Soil sensor
▬ IR heater
▢ High prov
▢ Low prov

Control
Heat
Water
Heat-Water

Forest, 3060 m

(a)

Recruitment to year 1
(# seedlings/seed sown)

☐ Control
🟥 Heat
🟦 Water
🟪 Heat-Water

Forest   Treeline   Alpine

(b)

Forest   Treeline   Alpine