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Title: Declines in low-elevation subalpine tree populations outpace growth in high-elevation populations with warming

Short Title: Subalpine tree range dynamics with warming

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Summary.

1. Species distribution shifts in response to climate change require that recruitment increase beyond current range boundaries. For trees with long lifespans, the importance of climate-sensitive seedling establishment to the pace of range shifts has not been demonstrated quantitatively.
2. Using spatially explicit, stochastic population models combined with data from long-term forest surveys, we explored whether the climate-sensitivity of recruitment observed in climate manipulation experiments was sufficient to alter populations and elevation ranges of two widely distributed, high-elevation North American conifers.
3. Empirically observed, warming-driven declines in recruitment led to rapid modeled population declines at the low-elevation, "warm edge" of subalpine forest and slow emergence of populations beyond the high-elevation, "cool edge". Because population declines in the forest occurred much faster than population emergence in the alpine, we observed range contraction for both species. For Engelmann spruce, this contraction was permanent over the modeled time horizon, even in the presence of increased moisture. For limber pine, lower sensitivity to warming may facilitate persistence at low elevations – especially in the presence of increased moisture – and rapid establishment above treeline, and, ultimately, expansion into the alpine.
4. *Synthesis*. Assuming 21st century warming and no additional moisture, population dynamics in high-elevation forests led to transient range contractions for limber pine and potentially permanent range contractions for Engelmann spruce. Thus, limitations to seedling recruitment with warming can constrain the pace of subalpine tree range shifts.

Introduction

Many plant species may not be able to migrate fast enough to keep pace with accelerating anthropogenic climate change. Observations and tools to reliably project these climate-vegetation disequilibria are lacking, yet they are critical to ecological theory and resource management. For example, tree species' ability to keep pace with the amplified warming occurring at high-elevation forest limits (Mountain Research Initiative EDW Working Group 2015) will depend on how fast expansion at the upper, "cool edge" proceeds relative to contraction at the lower, "warm edge" of subalpine forest (Hampe & Petit 2005). It is assumed that subalpine trees will move to higher elevations with climate change because low summer temperatures have been observed to limit tree growth above treeline (Korner, 2012, Rossi *et al.*, 2008). The fate of mountain forests is particularly important given anticipated widespread tree mortality (van Mantgem *et al.* 2009; McDowell & Allen 2015). Range shifts in high-elevation forest trees can alter the position of treeline with implications for water supply (Musselman *et al.* 2012), carbon sequestration (de Wit *et al.* 2014), alpine biodiversity (Gottfried *et al.* 2012; Pauli *et al.* 2012), and regional climate (de Wit *et al.* 2014). Density of trees and percent canopy cover are important determinants of winter snow pack and duration of retention into the spring, where high-elevation biodiversity depends on water provisioning provided by subalpine forests (Millar & Rundel 2016). Understanding dynamic forest change requires models that include dispersal limitation, long maturation times, climate-sensitive demographic rates (Jackson *et al.* 2009), and the experimental data to specify and test the models.

Recent advances in modeling range shifts have included dynamic populations (Dullinger *et al.* 2012, 2015; Conlisk *et al.* 2013; Fordham *et al.* 2013) and climate-sensitive processes (Chuine & Beaubien 2001; Crozier & Dwyer 2006), but their application lags far behind traditional correlative climate niche models (Franklin 2010; Dormann *et al.* 2012). While climate niche models outline a potential species range at some future period (Monahan *et al.* 2014), demographic models are needed to determine the timing of population changes that cause range shifts. In the extreme, population models determine whether a potential future range is consistent with species' demographic rates. Among existing demographic models, most rely on data from laboratory experiments that may not mimic field conditions (Chuine & Beaubien 2001; Crozier & Dwyer 2006) or vital rates from populations distributed along climate gradients (Fordham *et al.* 2013). Rare, *in situ* climate experiments that focus on distributional shifts, such as (Kueppers *et al.* 2016), offer a valuable source of data for parameterizing demographic models, and a novel approach to advance our understanding of the pace and extent of climate change-driven range shifts.

Because recruitment of new individuals is essential to population persistence in existing habitat and to colonization of new habitat, climate-driven changes in recruitment are likely to influence range shifts (Walck *et al.* 2011). Colonization can proceed quickly when propagules are plentiful, and dispersal and individual establishment rates are high, but can require decades or centuries for slow-growing, long-lived species with restricted dispersal and low or variable seed production (Kroiss & HilleRisLambers 2014). Recent studies show that juvenile trees often occupy a narrower climate niche than adults (Zhu *et al.* 2012; Dobrowski *et al.* 2015), with restrictions in juvenile ranges particularly pronounced in water-limited areas (McLaughlin & Zavaleta 2012; Dobrowski *et al.* 2015). However, previous models have typically ignored the difference in climate niche between adults and juveniles, except in limited cases with short-lived plants (Doak & Morris 2010). Given the long reproductive lifespan of trees, small changes in annual recruitment are likely inconsequential to population persistence, but large observed changes in recruitment with warming, such as the 11-95% decrease in relative recruitment seen in Kueppers *et al.* (2016), could affect population abundance and ranges. Understanding the population implications of climate-induced changes in recruitment requires consideration of these changes within the context of the trees' full life history.

At alpine treeline, many tree species are moving upslope in response to 20th century warming, but this response is not ubiquitous (Harsch *et al.* 2009), likely reflecting demographic lags or interactions between temperature and other factors, such as soil moisture. Low temperatures in subalpine forests are assumed to limit tree growth and wood formation (Rossi *et al.* 2008; Palacio *et al.* 2014), leading to a proposed global boundary for alpine treeline at elevations where average growing season temperature is ~6 °C (Korner & Paulsen 2004). However, from central Chinese forests (Wang *et al.* 2006) to Patagonia (Daniels & Veblen 2004), studies suggest that moisture availability influences treeline position, providing a potential mechanism for shifts downslope (Lenoir *et al.* 2010). Over longer timescales, Holocene warming caused treeline to occur at higher elevations in the western U.S. (Morgan *et al.* 2014) and Europe (Schwoerer *et al.* 2014), with exceptions in areas such as the Sierra Nevada of California, where treeline movement to higher elevation was limited by drought (Lloyd & Graumlich 1997). While observational studies have provided insights into how forests have responded to previous climate change (Carrara *et al.* 1991), future effects of rapid anthropogenic climate change may depart from historic trends due to slow demographic responses to warming, water availability, and their interaction (Williams & Jackson 2007).

Here we use stochastic, demographic models to test whether recruitment limitations observed in climate manipulation experiments are large enough to alter populations of Engelmann spruce and limber pine, two widespread North American subalpine conifers with very different life-history and dispersal strategies. Previous climate niche models have suggested that suitable climatic conditions for both species will emerge in what is currently alpine habitat (Rehfeldt *et al.* 2006; Monahan *et al.* 2014). We considered four model scenarios analogous to four experimental climate treatments (control, heated, watered, and heated and watered) across forest, treeline and alpine sites (Kueppers *et al.* 2016). We used 31 years of demographic observations in the same forest to parameterize adult demographic rates, holding adult survival rates constant across scenarios to explore the influences of recruitment on projected range shifts. Our goal was not to forecast populations of Engelmann spruce and limber pine under climate change, but rather to test the influence of changes in observed seedling recruitment on populations across sites and climate scenarios. We hypothesized that warming would yield reductions in low-elevation, warm-edge populations and delay or prevent wind-dispersed Engelmann spruce colonization in alpine sites given observed large decreases in Engelmann spruce recruitment with experimental warming across sites (Kueppers *et al.* 2016). For more drought-tolerant, bird-dispersed limber pine (Tomback & Linhart 1990), we expected a smaller effect of warming on low elevation populations and little delay in population establishment in the alpine given lower observed sensitivities, and even benefits, from warming. Given the observed sensitivity of seedling recruitment to water additions across the landscape, we expected increased summer moisture to enable population persistence at low elevation and facilitate upslope range expansion for both species.

Methods

Study species. Our two focal species are widely distributed in Western North America. Engelmann spruce (*Picea engelmannii* Parry ex. Engelm) occurs at high elevations up to treeline in the Rocky Mountains and in the Cascade Ranges. Limber pine (*Pinus 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 a shade-intolerant pioneer species. Limber pine produces fewer, larger, bird- and mammal-dispersed seeds compared to abundant, small, wind-dispersed Engelmann spruce seeds.

Demographic model overview. We constructed spatially-explicit, stage-structured meta-population models with environmental and demographic stochasticity (Akcakaya & Root 2005) separately for each species. We used an annual time step and a three-patch meta-population – with forest, treeline and alpine patches – connected through seed dispersal (Fig 1). Each of the modeled patches was defined as an elevation band, separated from the next patch by roughly 300 m, leading to high dispersal between patches. We parameterized the first four life stages, or "seedling" stages, using recruitment and survival data from climate change experiments replicated at three sites along an elevation gradient at Niwot Ridge, Colorado, U.S.A. (Kueppers *et al.* 2016). Thus, the first four seedling stages of the transition matrix are defined by seedling age, with survival probabilities given in Tables 1 and 2 (see *Seedling demographic data* section below and the supplemental materials for more details on model parameterization). We parameterized the adult growth and survival for individuals >4 cm in diameter-at-breast-height (dbh) from long-term demography data collected in five plots, also at Niwot Ridge (Smith *et al.* 2015). Under-constrained parameters (for large seedlings and small saplings) were set such that population growth rates in forest patches were consistent with observed adult population growth in these long-term demography plots. Other parameters were derived from the literature or selected based on model sensitivity analyses (see below). Individuals could progress through seedling and sapling stages to become reproductive adults (defined as dbh≥1cm) in as few as 15 years, with an average age at first reproduction of about 45 years for each species. Individuals could progress through the 34 reproductive, adult stages in as few as 35 years, with average residence times of 180 and 320 years for Engelmann spruce and limber pine, respectively. We included many adult life stages to ensure that individuals would not progress through their life-cycle at an unrealistically rapid pace (see *Adult demographic data* and the supplemental materials for explanation of parameterization). The four model scenarios were analogous to the four experimental treatments (control, heated, watered, and heated and watered), where only seedling parameters were changed across scenarios (all other model parameters were kept constant). For warming scenarios, heating effects were phased in linearly over 100 years. Models were run 1000 times for each scenario, with a 500-year model time horizon.

Seedling demographic data. We collected data on germination and annual seedling survival to the fourth year of life in common gardens that were experimentally manipulated with crossed heating and watering treatments (Kueppers *et al.* 2016). The experimental gardens were replicated across three sites on the eastern slope of the Rocky Mountains at Niwot Ridge, CO USA (Castanha *et al.* 2012): (i) a stand of reproductively mature trees near the low-elevation "warm edge" of subalpine forest, (ii) an open meadow surrounded by krummholz mats and low tree islands at treeline, the "cool edge" of subalpine forest, and (iii) an alpine meadow approximately 400 meters above timberline. Six 1000W infrared heaters arrayed around the perimeter of heated plots raised mean daily soil temperature during the snow-free periods, with larger increases in the forest (+3.8 °C), than in wind-swept alpine and treeline sites (+1.4 and +1.7°C, respectively) (Kueppers *et al.* 2016). These temperature increases are consistent with late 21st century projections for this elevation and region under an RCP4.5 scenario (Wang *et al.* 2012). Heating also extended the growing season and reduced summer soil moisture by 0.012, 0.012, and 0.016 m^3 water/m^3 soil at 5-10cm depth at forest, treeline and alpine sites, respectively. We designed the watering treatments (2.5 mm/week) to compensate for evaporative losses due to heating, adding water manually starting 2-3 weeks after snowmelt and ending in September. We sowed seeds annually and tracked the number of seeds sown and number of seedlings surviving to autumn of each year out to four years. These annual survival values were used to parameterize the first four seedling stages in the transition matrix. Seeds from high (3370-3570 m) and low (2910-3240 m) elevation seed provenances were sown and tracked separately (Kueppers *et al.* 2016), but we averaged across provenances to obtain the annual survivals used in the model (summarized in Tables 1 and 2 for Engelmann spruce and limber pine, respectively).

Adult demographic data. Adult survival was measured in five long-term observational plots (Smith *et al.* 2015) – BW2, BW3, MRS4, BL6, and MRS7 – first censused in 1982 and last censused in 2013. Each plot contained, on average, more than 400 permanently tagged trees (> 4 cm dbh), including four species: Engelmann spruce, limber pine, lodgepole pine (*Pinus contorta* var. *latifolia* [Engl.] Critch.), and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt). Plot elevations ranged from 2980-3260 meters and stand age was > 250 years. Plots were revisited every three years to record mortality until 1994 (e.g. 1985, 1988, 1991, and 1994), then again in 2007, 2010, and 2013. Diameter at breast height (dbh) was recorded in 1982 and 2007. Dead trees, as well as potential causes of mortality (e.g. the presence of beetle exit holes and beetle galleries), were recorded. Because we wanted to focus on the direct impacts of climate change, and not potential indirect effects of climate change on insect pests (Mitton & Ferrenberg 2012), the nine limber pine trees (and no Engelmann spruce) killed by bark beetle were excluded from the analysis.

To determine survival as a function of life stage, we divided the Engelmann spruce and limber pine trees measured from 1982-2013 into size classes based on dbh. Engelmann spruce stages ranged from 4 cm < dbh < 34 cm, with each stage in the transition matrix representing a 1 cm dbh increment. Limber pine stages ranged from 4 cm < dbh < 49 cm, with a 1.5 cm dbh increment. There were at least seven Engelmann spruce or four limber pine individuals (and typically more than 10) in each dbh increment less than 34 cm (for limber pine there were 17 individuals between 34 and 49 cm dbh). Average survival for each stage as a function of dbh was used to parameterize survival for the various adult stages (Fig 2). For both species, we found the largest individuals had slightly lower survival (Fig 2). This is consistent with studies showing that larger individuals are more susceptible to lethal biotic agents (Schoettle & Sniezko 2007; Hart *et al.* 2014), and windfall (Alexander 1987,Veblen *et al.* 2001). In specifying environmental stochasticity, we assumed a coefficient of variation for adult survival of 0.02, consistent with the long-term demographic data.

We used this same dataset to parameterize forbidden transitions (or zero elements in the vital rates matrix). No Engelmann spruce or limber pine individuals grew more than 1 cm per year (Engelmann spruce and limber pine maximum annual growth rates averaged over 25 years were 0.5 cm/yr and 0.4 cm/yr, respectively), nor got smaller, therefore we did not allow rapid growth, skipping a stage, or background transitions. Adult “survival” was divided into individuals staying the same size (82% and 90% for Engelmann spruce and limber pine respectively) and transitioning into the next larger size class.

Large seedlings and small saplings. Survival values for large seedling (> 5 years) and small sapling (dbh < 4cm) stages came from the literature (see supplemental material). Under-constrained parameters were set such that the modeled forest population growth rates (for trees with dbh > 4 cm) were 0.999 for Engelmann spruce and 0.995 for limber pine, respectively, under the control scenario in the forest. These population growth rates were based on the number of adult trees recorded in 1982 and 2013.

Carrying capacity. We chose a high carrying capacity – 37,500 adults (dbh >33cm for Engelmann spruce and 47cm for limber pine) in a one km^2 patch – in order to minimize the impact of demographic stochasticity. The density of trees was based on the maximum number of Engelmann spruce observed in a one-hectare patch, where smaller individuals were assumed to take up less than one "adult equivalent". Specifically, we assumed that seed-bearing trees between 1-4 cm dbh took up 10% the space of the largest trees (i.e. there could be 3,750 small saplings/ha or 375 large trees/ha), where this fraction increased linearly with dbh until 33 cm for Engelmann spruce and 47 cm for limber pine. (Other relationships, such as quadratics, between dbh and "space used" did not change model results.) Because there were roughly three times fewer limber pine per hectare than Engelmann spruce in censused plots, we assumed the initial forest population of Engelmann spruce was three times larger than limber pine. Specifically, the initial forest abundances were 16,500 and 4,100 Engelmann spruce and limber pine, respectively, and the initial treeline abundances were 11,300 and 3,800. In forest and treeline patches, the initial population was divided amongst the various stages consistent with the equilibrium distribution for each patch, with a larger fraction of large trees in forest patches compared to treeline patches.

During a given simulation, when the carrying capacity of the model was reached, size dependent mortality was imposed such that smaller individuals were more likely to die. Starting with the smallest seedlings, survival was reduced to 90% of its initial value. For that time step, if the carrying capacity was still exceeded after the extra mortality in the smallest stage, the next larger stage had survival reduced to 90% of its initial value. This was continued, moving from small to large stages, until the carrying capacity was no longer exceeded. In a growing population, this led to transient increases in population size with high densities of younger individuals and later self-thinning, consistent with dynamics observed for other high elevation conifers (Gendreau-Berthiaume *et al.* 2016).

Seed production and dispersal. A variety of studies show ample, but highly variable, seed production for Engelmann spruce, with most un-germinated seeds not surviving in the field to the following year (see supplemental material). We assumed that the largest Engelmann spruce individuals could produce 1,462 viable seeds per year. Limber pine produces fewer, larger, better-provisioned seeds that are also highly desirable to seed predators. We assumed that the largest limber pine individuals could produce 479 viable seeds per year. For both species, seed production increased linearly (based on Stromberg & Patten 1993) with stage starting with one seed produced when a tree was, on average, 45 years of age.

We assumed dispersal between the treeline patch and either the alpine or forest patch (and no dispersal between the alpine and forest patches) of roughly 0.05% of Engelmann spruce seeds and 0.5% of limber pine seeds. Engelmann spruce dispersal was based on Alexander (1987) who reported exponential decline of dispersing seed with distance. We could not find a study documenting limber pine dispersal with distance. However, long-distance dispersal has been reported for *Strobus* pines dispersed by corvids and small mammals (see supplemental material). Thus, we assumed greater overall dispersal for limber pine.

Sensitivity analyses. To evaluate the effect of alternate parameter choices, particularly for unobserved parameters, we conducted sensitivity analyses that considered lower dispersal (10% of original value), lower seed production (80% of original value), reduced sapling survival

(98% of original value) and reduced adult survival (98% of original value). Sensitivity tests found that population growth rates were most sensitive to small changes in adult survival, but that differences among climate scenarios (e.g., warmed, watered) were robust to model parameterization (see supplemental material).

Results

Population models parameterized with recruitment data from our climate manipulations reveal that observed climate-induced changes in seedling survival alone are sufficient to cause changes to mature tree populations across climate scenarios and modeled habitat patches (Fig 3 and Fig 4). For both species, mean forest abundances were half their initial value in the warmed scenario after 150 years (Fig 3e and Fig 4e), with little variation across model runs. For Engelmann spruce, warming drove the drop in mean abundance as control populations were maintained to 500 years (with considerable variability across individual runs in control populations). However, for limber pine, the population declines in the presence and absence of warming were due to observed high mortality in long-term forest censuses (Smith *et al.* 2015). Because both species are long-lived, 6% and 10% of the initial populations for Engelmann spruce and limber pine, respectively, were still present at the end of 500 years in the warming scenarios. For both species, watering, in the absence of warming, increased mean abundance in the forest as compared to the control scenario, with large variability across model runs. For Engelmann spruce, the warming and watering scenario resulted in population declines similar to the warming scenario (Fig 3f), whereas, for limber pine, the warming and watering scenario had higher mean abundance than the control scenario (Fig 4f). For Engelmann spruce, the control and watering scenario mean abundances plus or minus one standard deviation (gray and blue shaded areas in Fig 3ef) largely overlapped one another. Similarly, the warming and warming-watering mean abundance plus or minus one standard deviation also overlapped (red and purple shaded areas in Fig 3ef). For limber pine, the watering scenario mean abundance minus one standard deviation (bottom of blue shaded area in Fig 4f) did not overlap any other scenario by the end of the model time horizon.

Population growth in treeline patches was high under all climate scenarios, including the control scenario, indicating the potential for increases in tree density at the upper elevation limit of both species even without further warming (Fig 3cd and Fig 4cd). There was little difference in mean tree abundance across scenarios and little variability across model runs. The highest abundances at treeline, for both species, were for the watered scenario (Fig 3d and Fig 4d), pointing to the persistent effects of water limitation on population sizes. Sensitivity tests with reduced adult survival led to more separation in projected abundance across scenarios, with the watered scenario continuing to have the highest mean abundance (supplemental material). Growing treeline populations provided ample propagules for potential population growth of trees in the alpine.

For both species, in the absence of watering, the emergence of mature trees in alpine patches occurred long after declines in the forest (Fig 3a and Fig 4a), emphasizing the importance of demographic processes to the pace of upslope range expansion for these long-lived trees. With ample propagules and dispersal from the treeline patches, the emergence of mature populations under the control scenarios suggest that seed availability may currently be an important constraint to upward range expansion. Warming delayed the emergence of Engelmann spruce populations beyond the 500-year time horizon of our model runs and many individual simulations ended with zero mature trees in the alpine. In the presence of warming and absence of watering, the forest population of limber pine declined to half its initial abundance after 150 years (Fig 4e) and mean alpine abundance grew to half the initial forest abundance after 330 years (Fig 4a). Although higher mean abundances occurred in the warming scenario compared to the control scenario, there was a 180 year lag between limber pine abundance losses in the forest and abundance gains in the alpine. In the presence of warming and watering, mean alpine limber pine abundance grew to half the initial forest abundance after 280 years (Fig 4b) with no losses in the forest (Fig 4f). Overall, while mean alpine abundances diverged, there was considerable overlap in the standard deviations across model runs amongst all limber pine scenarios. For Engelmann spruce, there was also considerable ensemble overlap for all scenarios except the warming scenario.

Shorter mean dispersal distances contributed to slower alpine population growth for Engelmann spruce relative to limber pine. Across all scenarios, no Engelmann spruce alpine population grew to half the initial forest abundance, whereas, limber pine populations emerged in the alpine after roughly three centuries. Further, the two species differed in their relative ranking across model scenarios. For Engelmann spruce in the alpine, the negative effect of warming was stronger than the positive effect of watering. For limber pine in the alpine, a modest, positive effect of warming added to a large, positive effect of water. For both species, lowering dispersal to the alpine and decreasing adult growth rates at the treeline slowed, and nearly halted, alpine population growth due to the dependence of the alpine population on seed from maturing treeline trees (supplemental material).

Discussion

Observed variation in seedling recruitment across experimental sites was large enough to substantially affect high-elevation conifer populations over time, emphasizing the importance of climate-sensitive tree recruitment to shifts in adult distribution. High recruitment rates at the treeline site translated into high population growth rates, even under the control scenario, and could indicate a legacy of 20th Century warming, facilitation by established trees, or seed limitation under current climate conditions. Increasing populations at treeline are consistent with observed infilling at treeline (Harsch *et al.* 2009; Liang *et al.* 2016) and in subalpine meadows (Jackson *et al.* 2016) in some regions. However, increased recruitment at treeline sites, leading to overall population sizes higher than currently observed at treeline, could also indicate that we are overestimating sapling and adult survival, growth, and fecundity rates at treeline. Because our goal was to investigate the importance of climate-dependent changes in recruitment, we assumed that sapling and adult survival, growth, and fecundity were constant across elevations, likely over-estimating treeline and alpine population growth rates. Because of greater overall recruitment and large population growth rates at treeline, changes in recruitment due to warming or watering had minimal population-level effects. In contrast, in forest and alpine sites, the magnitude of recruitment changes across experimental treatments led to population differences across model scenarios.

Climate scenarios. As expected, for Engelmann spruce, large decreases in recruitment with experimental warming across sites (Kueppers *et al.* 2016) yielded smaller populations in forest and alpine patches, whereas for more drought-tolerant, bird-dispersed limber pine, warming had little impact on population establishment in the alpine or loss in the forest. Engelmann spruce declines in the forest and lack of colonization in the alpine suggest that the elevational extent of Engelmann spruce's range could contract in the coming centuries, if other vital rates were unable to compensate for low recruitment. With warming, alpine colonization by limber pine took roughly 300 years, and, in the absence of watering, lagged forest decline by 180 years. In the absence of warming, limber pine populations took even longer than warmed populations to emerge in the alpine, suggesting that limber pine may be better poised to extend the upper limit of its elevation range with climate change. Although we simulate expansion of both species into alpine patches, our results assumed that the alpine climate will only warm by 1.4 ^{o}C (consistent with realized warming in the field experiment) over the next 100 years and remain stable thereafter. Future climate change may occur more rapidly or temperature increases may be of a larger magnitude, challenging forest persistence and upslope expansion.

While global treeline position is correlated with temperature (Korner & Paulsen 2004; Korner 2012), we found that shifts in tree distributions may be critically dependent on moisture availability. Watered scenarios yielded the largest populations in nearly all cases, consistent with our original hypothesis and previous research showing moisture limitation to be a significant constraint even at cold-edge range limits (Daniels & Veblen 2004). Engelmann spruce seedlings have higher survival on moist, north-facing slopes relative to dry, south-facing slopes (Gill *et al.* 2015). Even for more drought-tolerant limber pine, greater recruitment was correlated with greater soil moisture and shorter growing seasons at and above treeline (Moyes *et al.* 2013) and second-year carbon assimilation was equally limited by temperature and moisture (Moyes *et al.* 2015). Thus, rapid upslope range shifts under warming could be expected where drought-tolerant species are present or there is greater summer moisture availability.

Species differences. Differences between the two species with respect to the effect of warming and the pace of alpine colonization suggest a potential shift in the composition of high-elevation forests unless other vital rates can offset the impacts of warming on recruitment. Limber pine is better able to benefit early from warming and establish in harsh micro-sites, whereas Engelmann spruce may require facilitation by established trees to overcome recruitment limitation (Germino *et al.* 2002; Maher & Germino 2006; Elliott 2011). In our models, warming restricted range expansion by Engelmann spruce but accelerated limber pine expansion, suggesting a future forest with relatively more limber pine than Engelmann spruce. Similar species-specific climate responses have been found in paleo-reconstructions of forest communities (Davis & Shaw 2001).

Demographic lags. Despite limber pine's eventual population emergence in the alpine under warming, it took roughly 300 years, highlighting the importance of model frameworks that incorporate time-explicit demographic processes. In the absence of increased moisture, there was a lag of almost two centuries between limber pine population decline in the forest and mature population emergence in the alpine. Previous projections of limber pine's climatic range based on niche models suggested that suitable climatic conditions will move upslope by 2100 (Monahan *et al.* 2014). Even when we assume survival and growth rates from lower elevation forests, our models suggested that the climate conditions conducive to limber pine migration will occur long before population emergence in new habitat, consistent with tree-ring based studies that showed lagged shifts in tree establishment due to climate from the 1950s (Elliott 2011). Time lags in population establishment or turnover also have important ecological and management implications. In the presence of additional stresses, such as the exotic white pine blister rust (Schoettle & Sniezko 2007) or the climate-mediated effects of mountain pine beetle (Bentz *et al.* 2010), limber pine may not emerge in formerly alpine environments even after long lags.

Variability across model runs. Although observed variation in seedling recruitment across experimental sites led to changes in the average population size across 1000 model runs, there was considerable variability among individual simulations. Except in the case of rapid population decreases in the forest, or rapid population increases at treeline, the standard deviation across model runs was large; in some cases the standard deviations of different climate scenarios overlapped. Large standard deviations in modeled population sizes were due to the high standard deviations in vital rates observed in the literature for survival, growth, and fecundity across sites and studies. Thus, across high elevation landscapes, for any given 1 km^2 (the assumed size of our modeled patches), our model predicted high variability in observed population sizes, where, for example, a hypothetical warmed and watered limber pine patch may have a similar population size as a watered patch. However, the means across these patches showed clear trends, consistent with experimental treatments. Thus, when 1 km^2 patches are aggregated across subalpine forests, our models suggest that warming- or watering-induced changes in recruitment will have a substantial average influence on populations of Engelmann spruce and limber pine.

Future directions. While we demonstrated the potential for delays in climate change-driven range shifts resulting from limitations to seedling recruitment and tree demographics, further work is needed to build data-driven models that include stage-specific, potentially compensatory, climatic responses. Our sensitivity tests showed that our models were sensitive to changes in adult survival (supplemental material). Emerging evidence suggests warming is increasing mortality of mature trees (van Mantgem *et al.* 2009; McDowell & Allen 2015; Smith *et al.* 2015), highlighting that our scenarios may be conservative with respect to negative effects of climate change on forest tree populations. Further, while historically slow tree growth rates at some treeline sites have been increasing in response to warming (Salzer *et al.* 2009), we used the adult growth and survival rates obtained in a forest (Smith *et al.* 2015) to parameterize treeline populations. Thus, we have likely over-estimated treeline population growth rates, and provided an optimistic scenario for upslope migration by Engelmann spruce and limber pine. Future models should incorporate the influence of climate on all life stages, especially when life stages respond differently to climatic changes (as in Doak & Morris 2010).

In addition to stage-specific, climate-driven vital rates, future models should also include genetic adaptation, and facilitation by established individuals. Our experimental work indicates that seed from low elevations has higher germination and seedling survival in treeline and alpine plots than seed from high elevations (Kueppers *et al.* 2016), suggesting that upslope migration may be limited by the fitness of local seeds. Advances in demographic modeling of distinct genotypes is required to assess whether genetic diversity can keep pace with climate change (Aitken *et al.* 2008). Projecting the pace of upslope migration should also incorporate inter-specific competition and facilitation, such as shrubs prohibiting conifer growth (Liang *et al.* 2016), corvids dispersing limber pine seeds (Tomback *et al.* 2005), or grasses influencing shade and moisture for Engelmann spruce (Germino *et al.* 2002). While there is much potential for further improvements, we have demonstrated that utilizing data from *in situ* climate manipulations can be used within such modeling frameworks to quantify the potential effects of recruitment limitation on the pace of distribution shifts.

Conclusions

Population models using climate-driven recruitment observed on a Colorado mountainside, highlight the important possibility that recruitment will drive transient range contractions in subalpine forests in Western North America over coming centuries. These findings reinforce the critical role of time-dependent demographic processes in determining the pace of population and distribution changes at both the leading and trailing edges of species ranges.

Author Contributions

E.C., M.G., and L.K. conceived model simulations; E.C. performed simulations and analyzed the data; C.C., J.S., T.V., and L.K. contributed data; E.C. and L.K. led and all authors contributed to writing the paper.

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Data Accessibility

Model results and models are archived in the Dryad repository: provisional doi:10.5061/dryad.q1f65 (Conlisk et al. 2017).

Figures

Figure 1. The model assumed three 1km^2 patches analogous to the three sites in the recruitment experiment: (i) an alpine patch with initially no individuals, (ii) a treeline patch with mostly small saplings and few large adults, and (iii) a forest patch with initially many adults. Dispersal between treeline and alpine patches and treeline and forest patches was set at 0.05% and 0.5% of seeds produced for Engelmann spruce and limber pine respectively.

Figure 2. Survival as a function of dbh for Engelmann spruce (gray circles) and limber pine (black squares). Resulting quadratic equations are as follows: $\text{Survival.}_{\text{Spruce}} = -1\text{x}10^{-5}\ \text{dbh}^2 + 0.0006\ \text{dbh} + 0.9925$ ($R^2 = 0.3502$) and $\text{Survival.}_{\text{Pine}} = -1\text{x}10^{-5}\ \text{dbh}^2 + 0.0009\ \text{dbh} + 0.9852$ ($R^2 = 0.4842$).

Figure 3. Abundance of mature Englemann spruce trees (>4 cm diameter at breast height, dbh) through time for warmed (red and purple lines) and unwarmed (black and blue lines) scenarios crossed with unwatered (left column) and watered (right column). Models included three patches: alpine (a, b), treeline (c, d), and forest (e, f) that interacted through dispersal. Patches were assumed to be approximately 1 km^2. Shaded areas delineate one standard deviation across 1000 model runs. Vertical lines show when the warmed or warm-watered scenario populations have declined to 50% of their initial abundance (solid) and when the alpine warmed or warm-watered scenario population has grown to 50% of the initial forest abundance (dashed). The horizontal arrows show the lag between the decline in forest populations and emergence of alpine populations in the warmed scenario. For Engelmann spruce, the alpine population does not grow to 50% of the initial forest abundance within 500 years, and thus the lag is >350 years.

Figure 4. Abundance of mature limber pine trees (>4 cm diameter at breast height, dbh) through time for warmed (red and purple lines) and unwarmed (black and blue lines) scenarios crossed with unwatered (left column) and watered (right column). Models included three patches: alpine (a, b), treeline (c, d), and forest (e, f) that interacted through dispersal. Patches were assumed to be approximately 1 km^2. Shaded areas delineate one standard deviation across 1000 model runs. Vertical lines show when the warmed population has declined to 50% of their initial abundance (solid) and when the alpine warmed and warm-watered scenario populations have grown to 50% of the initial forest abundance (dashed). There is no solid vertical line for the watering column because the forest population did not decline. The horizontal arrows show the lag between the decline in forest populations and emergence of alpine populations in the warmed scenario. The unwatered (left column) warmed and control scenarios lie on top of one another, thus, the black line cannot be seen.

Table 1. Observed Engelmann spruce mean annual recruitment and survival. Standard deviations follow the ±. Number of quadrant-year combinations (low- and high-elevation seed sources are combined) contributing to the mean is in parentheses. In the models, where data was not available (NA), values were assumed as described in the notes.

	First-year recruitment (seed to year 1)	**Second-year survival (year 1 to year 2)**	**Third-year survival (year 2 to year 3)**	**Fourth-year survival (year 3 to year 4)**
ALPINE				
Control	0.0481 ± 0.0738 (50)	0.5921 ± 0.3835 (25)	0.9000 ± 0.2108 (10)	1[1] ± NA (8)
Watered	0.0462 ± 0.0514 (50)	0.5340 ± 0.3786 (28)	0.8864 ± 0.1404 (13)	0.8408 ± 0.1833 (10)
Heated	0.0274 ± 0.0472 (50)	0.5368 ± 0.3711 (23)	0.8095 ± 0.2440 (7)	0.9583 ± 0.8555 (6)
Heat-Watered	0.0517 ± 0.0743 (50)	0.5695 ± 0.3524 (23)	0.7607 ± 0.3478 (10)	0.7936 ± 0.8874 (5)
TREELINE				
Control	0.0328 ± 0.0382 (50)	0.4717 ± 0.2680 (33)	0.7165 ± 0.3259 (22)	0.8636 ± 0.2335 (11)
Watered	0.0502 ± 0.0514 (50)	0.6059 ± 0.2398 (36)	0.8014 ± 0.2093 (25)	0.8484 ± 0.1945 (15)
Heated	0.0230 ± 0.0371 (50)	0.3903 ± 0.2764 (24)	0.6652 ± 0.4017 (11)	0.8555 ± 0.1410 (7)
Heat-Watered	0.0365 ± 0.0534 (50)	0.5183 ± 0.2741 (32)	0.7093 ± 0.3246 (18)	0.8874 ± 0.1418 (10)
FOREST				
Control	0.0324 ± 0.0588 (50)	0.0849 ± 0.1310 (14)	0.5167 ± 0.5008 (3)	1[1] ± 0[4] (2)
Watered	0.0219 ± 0.0337 (50)	0.1649 ± 0.1982 (15)	0.5833 ± 0.4640 (7)	0.7500 ± 0.5000 (4)
Heated	0.0008 ± 0.0046 (50)	0.2222 ± 0.3849 (0)	NA ± NA[2] (0)	NA ± NA[2] (0)
Heat-Watered	0.0020 ± 0.0081 (50)	0.2212 ± 0.3772 (5)	0.5 ± NA (1)	0 ± NA[3] (1)

[1] Where survival of 1 is reported, we used the previous year's survival in the model.

[2] The ratio heated-watered/watered was used to define the reduction in third- and fourth-year survival in going from control to heated in the model.

[3] We used the ratio of the heated-watered/watered for third-year survival to define fourth-year survival reduction as a function of heating.

[4] We used the standard deviation for third-year survival in control plots.

Table 2. Observed limber pine mean annual survival. Standard deviations follow the ±. Number of quadrant-year combinations (low- and high-elevation seed sources are combined) contributing to the mean is in parentheses.

	First-year recruitment (seed to year 1)	**Second-year survival (year 1 to year 2)**	**Third-year survival (year 2 to year 3)**	**Fourth-year survival (year 3 to year 4)**
ALPINE				
Control	0.1241 ± 0.1456 (50)	0.4829 ± 0.2891 (36)	0.6889 ± 0.3501 (24)	0.8020 ± 0.2216 (14)
Watered	0.1449 ± 0.1372 (50)	0.5778 ± 0.2610 (39)	0.6485 ± 0.2971 (27)	0.7721 ± 0.2466 (17)
Heated	0.1105 ± 0.1210 (50)	0.5113 ± 0.2507 (34)	0.7788 ± 0.2670 (24)	0.8372 ± 0.2729 (17)
Heat-Watered	0.1270 ± 0.1327 (50)	0.5884 ± 0.3108 (35)	0.8300 ± 0.2087 (22)	0.8459 ± 0.1647 (13)
TREELINE				
Control	0.1949 ± 0.1705 (50)	0.5343 ± 0.2952 (37)	0.7032 ± 0.2653 (25)	0.7786 ± 0.2039 (14)
Watered	0.1939 ± 0.1661 (50)	0.6907 ± 0.2550 (38)	0.8174 ± 0.2087 (27)	0.8324 ± 0.2301 (17)
Heated	0.1622 ± 0.1433 (50)	0.5296 ± 0.3033 (37)	0.8546 ± 0.1331 (22)	0.9164 ± 0.0837 (13)
Heat-Watered	0.1388 ± 0.1156 (50)	0.6451 ± 0.2800 (39)	0.7866 ± 0.2515 (26)	0.8950 ± 0.1355 (15)
FOREST				
Control	0.1064 ± 0.1100 (50)	0.1812 ± 0.2523 (35)	0.4187 ± 0.3598 (13)	0.8333 ± 0.4082 (6)
Watered	0.1420 ± 0.1380 (50)	0.3550 ± 0.2741 (36)	0.6110 ± 0.3258 (22)	0.7464 ± 0.3335 (15)
Heated	0.0419 ± 0.0635 (50)	0.2166 ± 0.2578 (27)	0.6243 ± 0.3319 (16)	0.8052 ± 0.4004 (11)
Heat-Watered	0.0529 ± 0.0706 (50)	0.2729 ± 0.2867 (27)	0.5866 ± 0.3301 (17)	0.9370 ± 0.1331 (13)

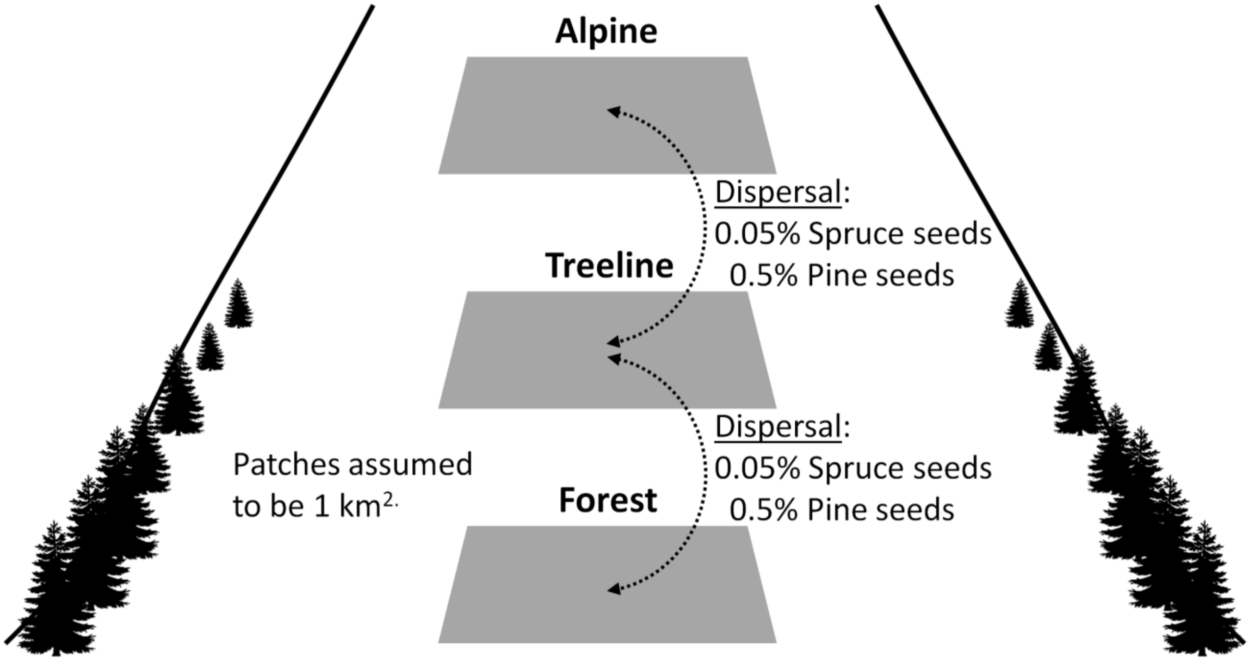

Alpine
Dispersal:
0.05% Spruce seeds
0.5% Pine seeds
Treeline
Dispersal:
0.05% Spruce seeds
0.5% Pine seeds
Patches assumed
to be 1 km^{2}.
Forest

Figure 1.

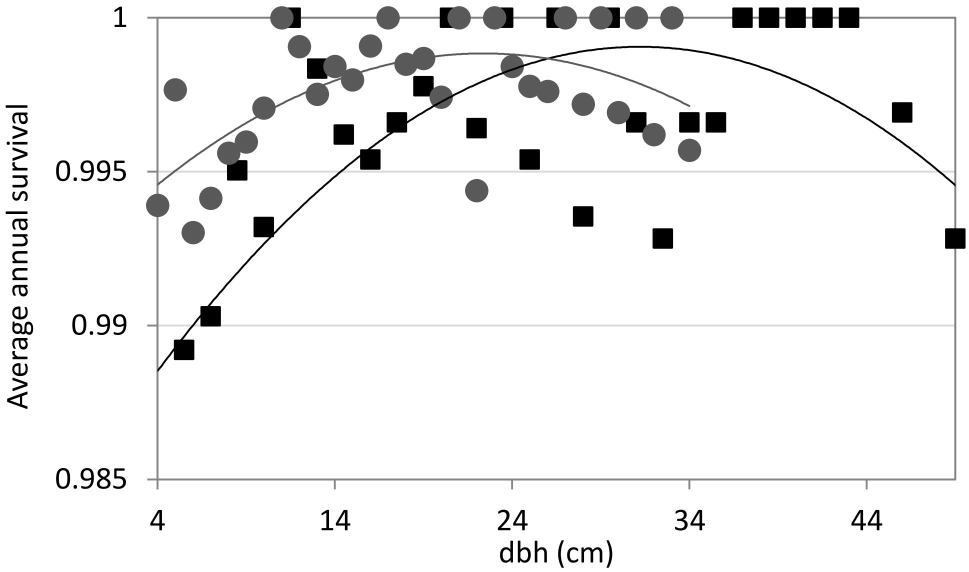
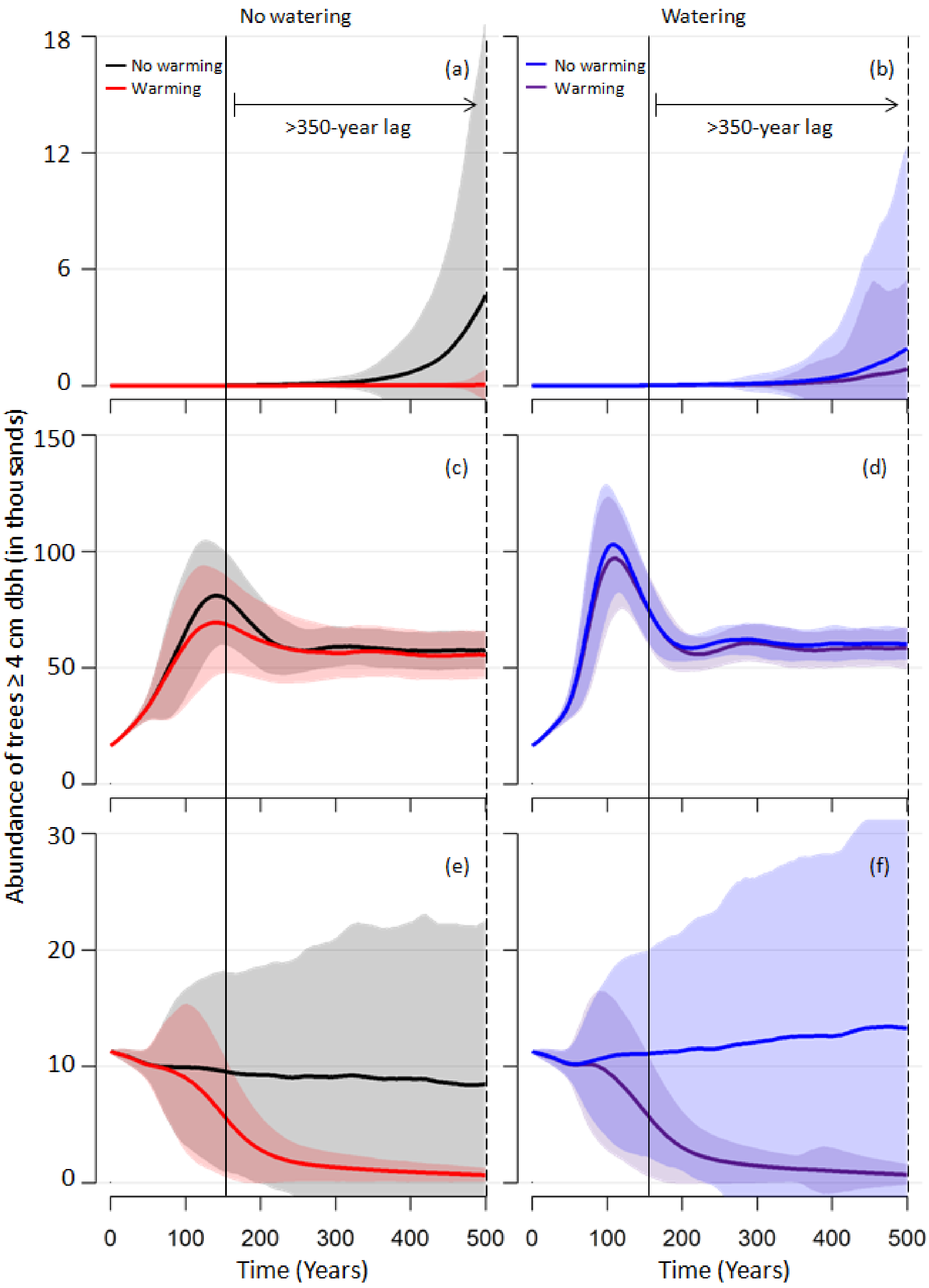
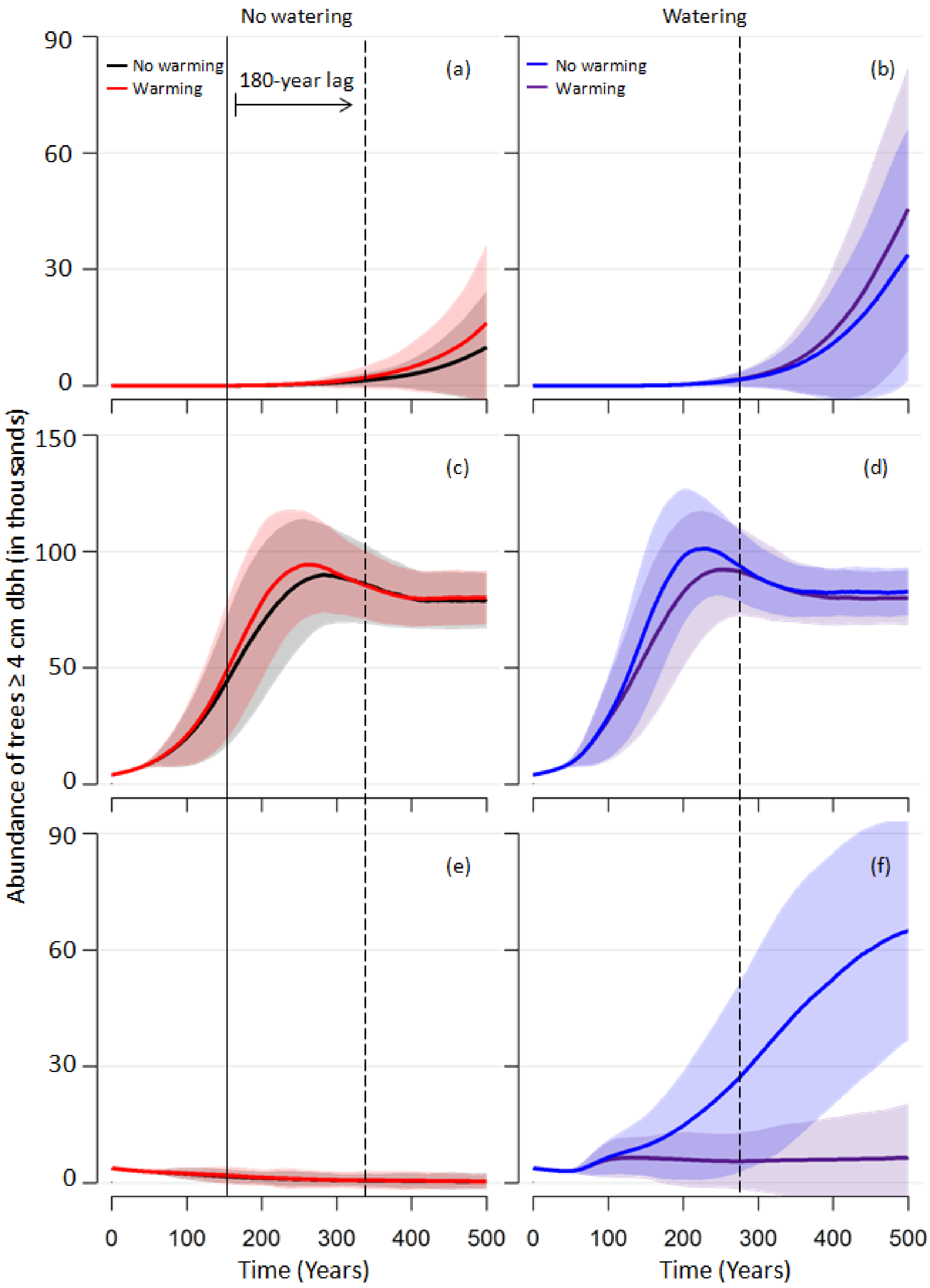


Figure 2.



769

770 Figure 3.



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772 Figure 4.