DR. AILENE ETTINGER (Orcid ID : 0000-0002-6228-6732)

Competition and facilitation may lead to asymmetric range shift dynamics with climate change

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Authors: Ailene Ettinger[1,2] & Janneke HilleRisLambers[3]

1. Ailene.Ettinger@tufts.edu; for correspondence: Department of Biology, Tufts University, Medford, Massachusetts, 02155, USA; Phone: 781-296-4821.

2. Arnold Arboretum of Harvard University, Boston, Massachusetts, 02131, USA

3. Department of Biology, University of Washington, Seattle, Washington, 98105, USA

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Abstract

Forecasts of widespread range shifts with climate change stem from assumptions that climate drives species distributions. However, local adaption and biotic interactions also influence range limits, and thus, may impact range shifts. Despite the potential importance of these factors, few studies have directly tested their effects on performance at range limits. We address how population-level variation and biotic interactions may affect range shifts by transplanting seeds and seedlings of western North American conifers of different origin populations into different competitive neighborhoods within and beyond their elevational ranges and monitoring their performance. We find evidence that competition with neighboring trees limits performance within current ranges, but that interactions between adults and juveniles switch from competitive to facilitative at upper range limits. Local adaptation had weaker effects on performance that did not predictably vary with range position or seed origin. Our findings suggest that competitive interactions may slow species turnover within forests at lower range limits, whereas facilitative interactions may accelerate the pace of tree expansions upwards near timberline.

Introduction

Ongoing climate change and the magnitude of projected future warming have fostered a renewed intense interest in the factors that determine species' ranges. Climatic factors (especially temperature) are thought to be important determinants of where species grow, survive, and reproduce; climate has therefore been the focus of many recent studies on range boundaries (Parmesan, 2006; Sexton et al., 2009; Chen et al., 2011; IPCC, 2014; Reich et al., 2015). Indeed, forecasts of how species' ranges will shift with climate change frequently rely *only* on projected climatic changes ("climatic envelope models") to predict future range boundaries (Pearson and Dawson, 2004; Ibanez et al., 2006; Swab et al., 2012). However, observed range shifts have not always matched what would be expected, based on climatic changes alone: upper and lower range limits of many species have undergone no change, or have shifted in the opposite direction as predicted with the past 100 years of

warming (e.g. Moritz et al., 2008; Harsch et al., 2009; Chen et al., 2011). Taking into account other climatic factors, such as changes in precipitation, may help explain surprising shifts in some cases (e.g. Tingley et al., 2012), but these variable responses suggest that focusing only on direct effects of climate may lead to inaccurate forecasts of the pace and magnitude of range shifts in a warming world.

Indeed, numerous non-climatic factors can also influence species' performance across their ranges (Davis et al., 1998; Jackson et al., 2009; Sexton et al., 2009; Wisz et al., 2013; Brown and Vellend, 2014). One such factor is population-level variation in sensitivity to climate, due to intraspecific genetic differentiation, which has been found in cold-hardiness, phenology (e.g. budset and bud burst), and growth rates (Chuine et al., 2006; Reich and Oleksyn, 2008; Chen et al., 2010; Leites et al., 2012; Alberto et al., 2013). For example, populations at range margins may have reduced genetic variation compared with central populations (Sexton et al., 2009); if so, they may lack sufficient variation to respond to directional selection by climate change, for example, favoring earlier phenology (Sheth and Angert, 2016). Thus, individuals and populations may respond differently to warming, depending on where they occur within a species' range (e.g. positively versus negatively, rapidly versus slowly, Angert et al., 2011).

Biotic interactions can also determine range limits, thereby influencing range shifts (He and Duncan, 2000; Arif et al., 2007; Jackson et al., 2009; Sexton et al., 2009; Wisz et al., 2013; HilleRisLambers et al., 2013; Svenning et al., 2014). Competition is the most widely documented biotic factor affecting range limits, but predation, parasitism, mutualisms, and other species interactions may also be important (Sexton et al., 2009; Wisz et al., 2013; Svenning et al., 2014). The presence of strong biotic constraints on species' distributions may result in range limits that are not sensitive to climate change, at least in the short term, if the abiotic factors influenced by climate change (e.g. temperature) are not primary limiting factors of species' performances at range boundaries. Alternatively, if populations at range edges encounter relatively weak negative interactions (e.g. competition) or relatively strong positive interactions (e.g. facilitation), compared with these interactions within the core of the range, then range expansion may be faster than predicted

by climate envelope models and other techniques that assume a constant strength of biotic interactions across the range (Van der Putten et al., 2010; Svenning et al., 2014). In short, biotic interactions are likely to have complex effects across species' ranges, leading to accelerated or decelerated range shifts compared to those expected from climatic change alone (Davis and Shaw, 2001).

It is likely that both population-level variation and biotic interactions influence species' range limits, and that they will interact with climatic factors to affect range shift dynamics with anthropogenic warming. However, the relative importance of each of these factors and the ways in which they interact are poorly understood. For example, most previous studies of competition and other biotic effects on range limits rely on observational studies and inferred interactions between species (e,g, Terborgh, 1971; Diamond, 1973; Jankowski et al., 2010). Though a handful of studies have empirically tested the role of biotic interactions in limiting species' performance at one range limit or another (e.g. Wethey, 2002; McCarthy-Neumann and Ibáñez, 2012; Brown and Vellend, 2014), we know of no studies that have done so across an entire range, let alone across multiple origin populations within a range (Sexton et al., 2009).

To address this knowledge gap, our study tests three critical hypotheses relating to the roles of population-level variation in climatic sensitivities (i.e. origin populations) and competition in determining species' range limits and affecting range shift dynamics with climate change:

1) *Niche hypothesis*: Performance (e.g. survival, growth) is highest in the middle of species' ranges (where climate may be 'optimal'), following classic fundamental niche theory and common assumptions by natural resource managers (Fig. 1a, e.g. Gauch and Whittaker, 1972; Rydin, 1997; Schwartz, 2012).

2) *Home-site advantage hypothesis*: Origin population affects tree responses to climate, such that tree performance is highest when individuals are grown in their "home" elevation and its associated climate (Fig. 1b, e.g. Clausen et al., 1948; Montalvo and Ellstrand, 2000; Bennington et al., 2012).

3)   *Competition-environmental gradient hypothesis*: Competitive effects dominate in more benign environments (at lower range limits in this case), whereas abiotic factors like climate constrain performance at upper range limits, where the environment is more stressful (Fig. 1c, e.g. Connell, 1961; Brown, 1984; Loehle, 1998).

These hypotheses, which are not mutually exclusive, relate to classic ecological theories, but they lack sufficient experimental field tests, especially in the context of forecasting range shift dynamics with climate change (Ettinger et al., 2011).

We address these hypotheses by examining effects of seed origin (low-, mid-, and high-elevation populations) and neighbor interactions (presence of canopy and understory vegetation) on tree seed germination, seedling survival, and seedling growth across an elevational and climatic gradient on Mt. Rainier, Washington, USA, spanning from 650-1650 m above sea level (Fig.1S). To our knowledge, this is the first study to empirically test the role of competition in limiting tree recruitment across the entire elevational range of multiple species. We transplanted tree seeds and seedlings from multiple populations of three common species (*Abies amabilis, Tsuga heterophylla, Tsuga mertensiana*) within and beyond their elevational ranges in areas that differed in the extent of aboveground competition, to address our three hypotheses. We focus on seeds and seedlings, since establishment is critical in determining the location of range boundaries and the pace at which range shifts will occur, particularly at the leading edge (Smith et al., 2003).

Materials and Methods

Study site, species and experimental design

To test our three hypotheses, we established a transplant experiment that spanned the elevational ranges of three focal species. Experimental sites were at seven elevations on Mt. Rainier (Fig. 1S), a 4,392-meter high volcano in the western USA. Strong climatic gradients exist on Mt.

Rainier: temperatures decline and precipitation increases with rising elevation (Franklin et al., 1988). Summers are dry, with most precipitation consisting of heavy snow that lasts into the growing season, particularly at high elevations (Franklin et al., 1988). We studied three dominant conifer species: *Tsuga mertensiana* (mountain hemlock), found from ~1200 m above sea level to treeline (>1600 m); *Abies amabilis* (Pacific silver fir), found from ~700m to ~1600m, and *Tsuga heterophylla* (western hemlock), occurring from sea-level (below the Park's boundary) up to ~1200 m.

To test the *niche hypothesis* (Fig. 1a), we monitored performance in seed addition and transplant plots that occurred in the middle of the range, and at, above, and below elevational range limits, for all species except *T. heterophylla* whose lower range limit is outside the park (Fig. 1a,1S, Franklin et al., 1988). This yielded seven transplant elevations (two focal species planted at all but the lowest elevation), with plots in five blocked replicates per elevation (20 plots per elevation; four per block). All seed addition and transplant plots occurred in closed canopy forests, except the highest elevation site, which was located in subalpine parkland, where "canopy gaps" are often small meadows (Fig. 1S).

To test the *home-site advantage hypothesis* and investigate effects of origin population (Fig. 1b), we collected seeds from populations located mid-range and at upper and lower range limits of all species in fall 2009 (except for *T. heterophylla*, for which we only collected mid-range and upper limit seeds). For seed addition plots, of which there were five per treatment per elevation (in blocked replicates, as described above), we scattered 50 seeds per species per origin in each seed addition plot in October 2010. Thus, the total number of seeds varied from 100-150 seeds per species, depending on the number of origin populations (50 seeds per origin population). For transplant plots (which were adjacent to seed addition plots), we planted 15 (for *A. amabilis* and *T. mertensiana*) or 16 (for *T. heterophylla*) total seedlings per species per plot: five seedlings per origin for *A. amabilis* and *T. mertensiana*, and eight seedlings per origin for *T. heterophylla*. Seedlings were grown at the University of Washington in Seattle for four months, then transplanted into plots on Mt. Rainier in October 2010, and watered at the time of transplant only (see Appendix S1 for propagation details).

To test the *competition-environmental gradient hypothesis*, we imposed different competition treatments within each block, which included fully factorial treatments of canopy (presence and absence) and understory (presence and absence). Thus, plots were established in forest canopy gaps (i.e. small patches with canopy absent) paired with non-gaps (i.e. canopy present), and each gap/non-gap pair constitutes a block; understory presence was manipulated within plots. Non-gap sites were established under closed canopy 10 m from paired gaps (which were located first) in a random direction. Blocks were separated by at least 20 m. Within each gap and non-gap, we established paired 0.25 m^2 plots and removed all understory aboveground competition within a half-meter radius around one plot per pair. We defined "understory" as vegetation less than two meters in height; vegetation removals were maintained monthly for the 2011 and 2012 growing seasons.

We censused germination in seed addition plots every month from May through October 2011. We do not report on the growth and survival of these germinants, as very few seedlings remained since mortality was extremely high after one season (only 0.10 germinants per origin population per species, on average per plot, survived to the beginning of the second growing season; standard deviation=0.68). Also, it should be noted that we did not explicitly test the viability of these seeds, nor did we quantify post-dispersal seed predation. Our germination measures therefore represent net germination from a given number of seeds per origin; with a lack of germination resulting from a variety of factors, including lack of viability and *in situ* seed predation. We also quantified germination of seeds collected from the same species and origins in the greenhouse at University of Washington, and provide this information for comparison (Fig. S3.1, Appendix S3).

We censused transplant seedling survival in transplant plots twice annually (spring and fall) in 2011 and 2012, and conducted a final census in fall 2013. We measured and analyzed transplant height (from ground surface to apical bud) annually in the fall. Some height measurements declined over time; these measures of 'negative' growth were due to transplant plugs sinking and litter and duff accumulating on top of the root crown (personal observation - this occurred at all sites). We found that height from the root crown to apical bud (measured at the final census), which was always greater than field-measured heights, was strongly correlated with above-ground field-measured height

(r=0.87, *P*<0.001), with a mean difference between these two heights (i.e. a mean amount of sinking) of 0.91 cm (SD=0.94, n=822). For our analyses, we used field-measured heights to calculate annual height increment (see Statistical Analyses section for details).

Microclimate, light, canopy cover, and soils

We quantified a series of environmental factors at each experimental site. We did this to verify that experimental sites at different range positions spanned the climatic gradients we assumed they did and that competition treatments modified light availability, as well as to understand whether canopy and understory vegetation affect microclimate (Ford et al., 2013). We used HOBO® Pendant loggers to collect measurements of soil surface temperature every two hours throughout the growing season (measurements were collected every three hours during the dormant season). These measurements were used to calculate snow duration and growing season length, which we define as the number of days with an average temperature above 5°C, for each plot.

We also quantified other abiotic and biotic factors, including light, canopy cover, and soil characteristics, which may affect seedling survival and growth and are likely to vary within and among plots and treatments. Prior to removing any competition or planting any seeds and seedlings in plots, we quantified the percent cover of ground surface material in each plot (e.g. bare soil, wood, leaf litter, moss). Visible light was measured every two hours during the growing season, using HOBO® Pendants (data were collected every three hours during the dormant season). We also measured photosynthetic active radiation (photon flux density) and soil moisture (volumetric water content, using a Decagon Devices EC-5 Soil Moisture Sensor) in each plot multiple times during the 2011 and 2012 growing seasons. We quantified percent canopy cover with a densiometer and collected soil samples from each gap and non-gap in September 2011. Five 15 cm-deep soil cores were collected from each gap and non-gap, and depths of O and A horizons were measured in each core. Soil cores were pooled by each gap/non-gap within a block, and the dry combustion method was

used to measure organic content and total carbon (C), hydrogen (H), and nitrogen (N) content (Perkin Elmer CHN/O analyzer, model 2400).

Statistical analyses

To test our hypotheses about the potentially interactive effects of range position, seed origin, and competition (canopy and understory presence), we fit statistical models to our performance metrics: seed germination, seedling survival, and seedling growth data. Because we were interested in dynamics at specific range positions (e.g. upper vs. mid-range vs. lower) and our hypotheses related to performance responses at different locations across species' ranges, we used range position as a categorical explanatory variable. A significant effect of range position, with reduced performance at and beyond range limits (i.e. a unimodal response) would support the *niche hypothesis*. A significant interaction between range position and seed origin, such that seeds and seedlings from each seed origin germinated, survived, or grew most at the locations from which they were collected would support the *home site advantage hypothesis*. An interaction between range position and either (or both) of the competitive treatments (canopy and understory), such that competitive effects on performance were greatest (and negative) at and below range limits, would support the *competition-environmental gradient hypothesis*.

We present models with range position and competition as categorical explanatory variables (as opposed to models that included microclimate or light as continuous explanatory variables) as our primary models of inference for two reasons. First, this framework allowed us to directly test our hypotheses about the effects of range position and competition on performance. Second, although we quantified some of the abiotic factors that vary with elevation (e.g. temperature, snow duration) and one resource for which trees are likely to compete (light), these may not represent all climatic variables that vary across range positions nor all the resources for which seedlings compete. To verify that our results are consistent with climatic variables (e.g. growing season temperature) and resource levels (light) known to affect seedling performance and thought to vary with our categorical

explanatory variables, we also fit and present models using continuous climatic and light predictors of germination, growth and survival, as described in Appendix S2 – results were qualitatively similar to those presented here.

We fit generalized linear mixed-effects models with successful germinants (out of total sowed seeds) as binomial response variables to assess germination responses, and included a block random effect (intercept-only structure). Our models included range position, seed origin, understory, and canopy presence, all 2-way interactions, and a 3-way interaction between range position, understory, and canopy. Because previous work suggests that moss can affect conifer establishment (Harmon and Franklin, 1989), we also compared these models to models that included a covariate of moss cover (percent of plot ground surface covered by moss at the start of the experiment), using AICc.

For survival of transplants, we fit accelerated failure-time models, using lognormal distributions and accounting for interval- and right-censoring (Therneau and Grambsch, 2000; Therneau, 2015). Our models included range position, seed origin, understory, and canopy presence, all 2-way interactions, and a 3-way interaction between range position, understory, and canopy. We were unable to include random effects of block in these models, as this method has not been developed for interval-censored data in available R packages (Therneau and Grambsch, 2000; Therneau, 2015). However, results were qualitatively similar to generalized linear mixed-effect binomial models (not shown) performed on individual censuses that did account for the non-independent nature of individuals occurring in the same block. We chose to model survival times instead of survival at a particular census date to model mortality rates over the three years of the experiment.

For growth, we fit linear mixed-effects models with a response variable of annual height increment: (final height-initial height)/number of years of growth. Growth was therefore quantified for all individuals that survived at least until the first census in which growth was measured (i.e. after one year). For individuals that survived multiple years (one, two, or three years), annual growth increment represents average annual growth across the growing seasons it was alive. We also analyzed our data using relative growth rate measures, and results were qualitatively similar (not shown). We included a block random effect (intercept-only structure) to account for non-

independence. Our growth models included the same main effects and interactions as survival models – i.e. range position, seed origin, canopy and understory presence, all 2-way interactions, and a 3-way interaction between range position, canopy presence, and understory presence.

We tested how elevation, canopy presence, and understory presence affected microclimate and light by fitting generalized linear mixed-effect models for snow duration, growing season length, and light each as response variables and with random effects of block and year (intercept-only structure). Our models included elevation, understory, and canopy presence, all 2-way interactions, and a 3-way interaction between elevation, understory, and canopy. We then tested for significance using type-III tests. Canopy cover and soil characteristics were collected in one year, at the block level (rather than plot level), so we used linear models with only elevation, canopy presence, and their interactions as explanatory variables, with no random effects of block or year.

We fit all statistical models in R, Version 3.2.4 (R Core Team, 2016), using the glmmADMB package for binomial generalized linear mixed-effects models for germination (Skaug et al., 2016-01-19), the 'survival' package for accelerated failure-time models (Therneau and Grambsch, 2000; Therneau, 2015), and the 'lme4' package for linear mixed-effects models for growth (Bates et al., 2015). R code can be found in Appendix S4.

Results

Focal species performance (germination, survival, growth)

Performance varied with the range position at which individuals were planted, for nearly all vital rates and species (Fig. 2). Range position explained a significant amount of variation in germination for *A. amabilis*, and in transplant survival for all three species (Fig. 2); however, there were no clear trends with range position for these vital rates (Fig. 3) – either linear or monotonic (as would support the *niche hypothesis*). Transplant growth generally declined at higher elevations for *A. amabilis* and *T. mertensiana* (Fig. 3g&h); it did not vary strongly with range position for *T. heterophylla* (Fig. 2c, Fig. 3i). In keeping with these results, model selection suggested that models with continuous growing season length explanatory variables (and light; as opposed to range position

and categorical competition) better explained growth of all three species (i.e. AICc values were lower). Continuous microclimate variables were not good predictors for germination (i.e. coefficients were not significantly different than zero, and null models fit better than continuous models with microclimate variables) nor for survival (i.e. AICc values for these models were higher than for categorical models). In all, results from models fit with continuous microclimate (and competition) explanatory variables were qualitatively similar to the categorical model results we present - see Appendix S2 for details.

Origin explained a small but significant amount of variation in performance for at least one vital rate for each species, either alone or by interacting with range position or competitive environment. Origin had significant effects on germination for *A. amabilis* and marginal effects for *T. heterophylla* (Fig. 2, Table 1). Effects of origin and/or interactions with origin were statistically significant ($P<0.05$) for two vital rates of *A. amabilis*: germination and survival. Germination was highest for upper limit populations in 2011 (14.5%, across all planted elevations of this species), more than four times as high as mid-range populations (3%, Fig. S3.1). Survival was greatest for mid-elevation origin populations of *A. amabilis* (614 days, compared with 517 days for lower limit and 581 days for upper limit populations). In *T. heteropyhlla,* effects of origin had statistically significant effects on growth, but only through its' interaction with canopy presence, with upper origin populations showing higher growth than mid-range populations with canopy present. In *T. mertensiana*, effects of origin were statistically significant only through interacting with range position for survival (see below).

Significant interactions between range position and origin, which would be required for local adaptation, occurred for germination and transplant survival in *A. amabilis* and for survival in *T. mertensiana*. However, individuals did not always perform best in locations closest to their origin (as in the *home-site advantage hypothesis*), but both species did show a general pattern of greater survival at high elevations for upper limit origins compared with lower limit origins (Fig. 3). Range position-origin interactions were insignificant for all vital rates in *T. heteropyhlla* (Fig. 2, Table 1).

Competitive environment explained a large amount of variation in performance for all species, but not all vital rates (Fig. 2, Table 1). Canopy and understory presence did not significantly affect germination in any species, but negatively affected survival and growth at nearly all range positions within the current ranges of the three species (i.e. up to 1603m above sea level; Fig. 4). There was also a significant interaction between competitive environment and range position for growth and survival; however, negative competitive effects on survival and growth were not consistently greatest below lower range limits (as would be expected in the *competition environmental gradient hypothesis*). Above the high-elevation upper limits of *A. amabilis* and *T. mertensiana,* effects of canopy and/or understory presence were positive for both survival and growth (Fig. 4). There were no significant effects of canopy nor of understory on germination (positive or negative, Table 1, Fig. 4). We found qualitatively similar results in models including light (instead of competition treatment) as an explanatory variable (see Appendix S2).

Additional germination analyses

In our greenhouse germination trials, germination rates, which were much higher than field-observed rates, varied by seed origin for all three focal species (Fig. S3.1). Origin-level patterns of germination in the field matched those in the greenhouse. For example, *T. mertensiana* seed collected from the lowest elevation had the highest germination rates in both the greenhouse and the field (Fig. S3.1a & d), and *A. amabilis* from the lowest elevation had the highest germination rates in both the greenhouse and the field (Fig. S3.1b & e). We also examined the effects of moss on germination, and found that it had significant effects for two of the three species: *A. amabilis and T. heterophylla*. Moss was included in the best-fit model for these two species, and thus is included in the models we interpret and show in all tables and figures here. Moss had a negative effect on germination for *A. amabilis*, and a positive effect on germination for *T. heterophylla* (Table S2). In neither case did the addition of moss as a covariate change our results qualitatively; for example, the sign of main effects did not change with the addition of moss.

Microclimate, light, canopy cover, and soils

Growing season length decreased with elevation, and canopy had a positive effect on growing season length at and above 1064 m in elevation, but not at lower elevations (i.e. there was a significant interaction between elevation and canopy, Table 2, Fig. 5). Snow duration increased with elevation and was negatively affected by canopy presence across the elevational gradient, although the negative effect was stronger at high elevations (Table 2, Fig. 5). Understory did not significantly affect growing season length or snow duration (Table 2). Light levels were negatively affected by both canopy and understory vegetation presence, with light levels and the magnitude of effects of vegetation on light varying slightly among elevations, but not in a consistent way across the elevational gradient (Table 2, Fig. 5). Soil moisture increased with elevation and was not affected by canopy presence, except at 1676 m (the highest elevation), where it was negatively affected by canopy presence (Table 2S). Total soil carbon varied by site, but not in a consistent way across the elevational gradient; total hydrogen and nitrogen levels increased with elevation; none of these were affected by canopy presence (Table 2S).

Discussion

Overall, our results imply that climate constrains performance at higher elevations for some life history stages and species, but that performance of our focal species did not simply peak at range centers as the commonly accepted *niche hypothesis* assumes. Instead, tree-to-tree interactions and seed origin influenced recruitment in ways that could have important implications for range shift dynamics. For example, recruitment varied by seed origin, and, although the magnitude of effects did not support the *home-site advantage hypothesis*, it is likely to add complexity to range shift dynamics. Our results offer partial support for the *competition-environmental gradient hypothesis*: we found that competition had uniformly negative effects within and below range limits. These effects did not get progressively more negative at lower elevations, as we expected under the *competition-environmental gradient hypothesis;* however, the negative effects did switch to positive interactions above upper

range limits (for two species). This observed facilitation implies that the balance between negative tree-to-tree interactions (within and below the range of a species) and positive tree-to-tree interactions (above upper range limits) might drive non-linear dynamics and asymmetric range shifts with climate change. We discuss these points in more detail below.

Niche hypothesis

Our results do not support niche theory, which assumes continuous, monotonic response curves, with optimal performance and abundance in the middle of species' ranges (Gauch and Whittaker, 1972; Rydin, 1997; Heikkinen and Makipaa, 2010). Instead, focal species frequently experienced their lowest germination and survival (across all competition treatments and origins) in the middle of their ranges; with higher germination and survival at one or both range limits (Fig. 3). Similarly, the greatest height growth increment was observed at the lowest elevations for all species (Fig. 3). These findings, combined with the many other studies that have also failed to observe peak performance at range centers, suggest that hypotheses based on niche theory need to be re-evaluated and should not be used as a basis for conservation and natural resource management action (Sagarin et al., 2006; Sexton et al., 2009). These include assumptions that speciation is more likely to occur at range edges, that populations in the center of species ranges are sources whereas edge populations are sinks, and that central populations are more critical to protect and monitor than edge populations (Sagarin et al., 2006).

Our results also suggest that current climate may not be the primary determinant of range limits for conifers on the south side of Mt. Rainier. For example, we did not find strong evidence that climate reduces performance (i.e. germination, survival, and growth), regardless of competitive environment, at and below current lower range limits, Fig. 3). At upper range limits, evidence for climatic controls on tree performance was mixed, differing for survival versus growth. On the one hand, we observed that tree growth declined with rising elevation, particularly for *T. mertensiana* and *A. amabilis* (Fig. 3), as expected if the increasing climatic stress along this gradient limits growth.

Indeed, we found positive effects of growing season length on growth for all focal species (Appendix S2, Table S2.2). This is not surprising, given that the heavier snowpack, shorter growing season lengths, and lower temperatures found at higher elevations are commonly thought to limit tree growth in the mountains of the Pacific Northwest (Peterson and Peterson, 2001; Nakawatase and Peterson, 2006; Ettinger et al., 2011). On the other hand, we observed higher survival at and above upper limits compared with range centers for *T. mertensiana* and *A. amabilis* (Fig. 3), counter to our expectation that overall survival would be lower above species' natural ranges if climate determines species' range limits (Fig. 1a). In our model comparison, we found that models with continuous climatic explanatory variables were poor predictors of survival, compared with the categorical models. This further suggests that climate (at least the climate variables that we measured) is not the primary limitation on tree seedling survival at all range limits; rather, other, unmeasured differences between range positions drive variation in survival across the range.

In all, our results suggest that non-climatic factors also affect recruitment at range limits, and that current adult tree ranges do not overlap perfectly with their climate niches. There are multiple potential reasons for this. First, there has likely been warming since the establishment of present-day canopy trees (Graumlich and Brubaker, 1986; Dunwiddie, 1986). In addition, juveniles are likely to have narrower niche requirements than adults (i.e. the "regeneration niche," Grubb, 1977; Jackson et al., 2009), and adult trees were used to determine the observed range boundaries (Franklin et al., 1988). Furthermore, our studies of juvenile tree performance represent a small snapshot in time, and recruitment can be highly variable among years (Clark et al., 1999). Kroiss & HilleRisLambers (2015) documented highly variable conifer seed production and germination rates among years at Mount Rainier. Our greenhouse germination trials suggest that seed viability may also vary from one year to the next (Fig. S3.1 in Appendix S3), and such annual variations may affect observed responses to climate and competition.

Home-site advantage hypothesis

We found little evidence that populations were adapted to local climate, nor that population differences constrained performance at range limits, despite our finding that origin population affected juvenile tree performance. Specifically, origin explained a statistically significant amount of variation only in some vital rates (Fig. 2, Table 1), and, even in these cases, there was not a consistent origin by location interaction, such that populations always performed best in locations closest to those from which they were collected (Fig. 3). For example, *A. amabilis* individuals from upper limit populations had higher germination and growth than those from other origins, even when planted at low elevations, far from their origin (Fig. 3, Fig. 1S). Moreover, origin population contributed more to variation in seed germination than to variation in transplant survival and growth vital rates, for which effects of elevation, competition, and their interaction were more important (Fig. 2, Table 1). This implies that origin population plays a less important role as seedlings establish and grow.

These results may seem surprising, given that other studies have found strong effects of origin (often called "provenance") on conifer growth when grown in common gardens (e.g. Carter, 1996; Leites et al., 2012; Reich et al., 2015). However, our study differs in several key ways that might explain these divergent results. First, many of these previous studies were focused on different species or life stages, rather than seedlings of the species we investigated; and it is known that performance varies by species and across life stages in its response to climate and other factors (Ettinger and HilleRisLambers, 2013). Second, although our focal populations spanned large climatic gradients, they are located fairly short geographic distances from one another (maximum 27 kilometers - Fig. 1S), especially relative to potential pollen dispersal distances: conifer pollen can disperse and remain viable for distances at least as great as 36-75 km (DiGiovanni et al., 1996; Williams and von Aderkas, 2011). This suggests that local adaptation to climate may be less important for altitudinal range shifts than latitudinal range shifts. Third, we focused on long-lived species, with canopy trees at our study sites being at least 300-800 years old (Franklin et al., 1988). Individuals from which seed were collected thus established at a time when climate likely differed from current climate (Dunwiddie, 1986). Therefore, our results may reflect that current distributions of species or populations are not at

equilibrium with the current climatic conditions; such nonequilibria may result in complex dynamics not forecasted by climate envelope models that do not incorporate population level variation in performance (Yackulic et al., 2015).

Competition-environmental gradient hypothesis

In contrast to the subtle and complex effects of origin population on juvenile performance, we found uniformly strong competitive effects on performance in closed canopy forests, especially for transplant survival and growth (Fig. 4). For example, canopy presence had large negative effects on transplant survival and growth of all species throughout most of their ranges (Fig. 4, Table 1). Thus, our results partially support the *competition-environmental gradient hypothesis* of increased competition near lower range limits (Fig. 1), for some species and vital rates (e.g. effects of canopy competition on *T. mertensiana* survival and *A. amabilis* growth, Fig. 4, Table 1). Areas with canopy present experienced low light levels (Fig. 5, Table 1S); thus, lower growth likely resulted from the lower photosynthetic rates that seedlings could achieve with this competing vegetation present. In support of this idea, light was included as an important explanatory variable in all best-fit growth models with continuous explanatory variables (Appendix S2). Because models including categorical canopy and understory presence (as opposed to light) better explained transplant survival (all species), competition for resources other than light (or other unmeasured environmental factors) are also likely to be important.

Presumably, the reduced growth caused by competitive interactions (light-mediated or otherwise) could slow the displacement of cold-adapted species by warm-adapted species (e.g. displacement of *Abies amabilis* by *Tsuga heterophylla* and other species as climate warms), unless adult trees die quickly and competitive pressures decrease. However, such changes are unlikely to occur rapidly, as tree species generally have low mortality (especially in our study system, Larson and Franklin, 2010) and can be relatively insensitive to climate at their lower range limits (Ettinger and HilleRisLambers, 2013). Thus, recruitment and upward range expansion of warm-adapted trees seems

likely to lag rapid rates of climate change, due to competitive interactions, at least in the absence of large-scale disturbance events that result in massive adult tree mortality.

Our results also imply that competition is not the only adult-juvenile interaction likely to influence range shifts in this system. We found that competitive interactions at low elevations changed to facilitative at high elevations: transplant survival and growth above the upper range limits were much greater under canopy than in the open for the two high-elevation species (*A. amabilis* and *T. mertensiana*, Fig. 4). Our data are consistent with strong abiotic stress (climate) driving upper range limits for these focal species (e.g. Connell, 1961; Brown, 1984; Loehle, 1998), and with canopy trees facilitating juvenile performance by altering microclimate in this harsh environment at high elevations (e.g. Holmgren et al., 1997). Canopy presence increased the growing season length (i.e. the number of days reaching temperatures above 5°C) by 31% at our highest elevation, but had no effect on growing season length at low elevations (Fig. 5b). It is also possible that growth and survival of seedlings in close proximity to adult trees at high elevations benefited from photoprotection by the canopy and/or a greater density of mycorrhizal symbionts, which may have been absent or reduced in abundance in the herbaceous-dominated montane meadow patches where adult trees were absent (Adams et al., 2002; Jumpponen et al., 2002; Zurbriggen et al., 2013).

Regardless of the mechanism, these facilitative interactions may introduce a local positive feedback between climate change and tree seedling performance, with increased warming eventually resulting in greater tree density, which increases growing season length and seedling recruitment even more. Such feedbacks could result in nonlinear range expansions with climate change: initially slow responses could be followed by a rapid encroachment of high elevation subalpine meadows by trees, once a threshold tree density is surpassed. We believe these types of facilitative interactions may be common in many ecosystems (although not always mediated by impacts on snow and growing season length), because competitive interactions have been found to switch to facilitative in diverse harsh environments (Callaway, 1998; He et al., 2013; Grant et al., 2014). Adding further complication,

however, is the observation that shifts in plant-plant interactions from facilitation to competition (or vice versa) can also be caused by extreme climatic events, such as drought or heavy precipitation events, and the nature of these shifts depends on species identity and on plant community composition (Grant et al., 2014).

Implications for range shift dynamics

In total, our study suggests that climate change induced range shifts are likely to be substantially more complex than predictions based on climate alone, due to non-climatic factors, especially biotic interactions. Commonly used climate envelope models (also called species distribution models) assume that climate is the primary factor determining species' range limits, and that range shifts will proceed at the pace of climate change (Pearson and Dawson, 2004; Swab et al., 2012). However, results of many studies (including this one) call into question the assumption that climate is the sole determinant of range limits, given inconsistent evidence that performance uniformly declines at and beyond range limits (especially lower range limits – Fig. 3) and ample evidence that biotic interactions can also constrain performance at range limits (e.g. Connell, 1961; Harley, 2011; Brown and Vellend, 2014). Even if climate is ultimately responsible for range limits (albeit indirectly), our results imply that non-climatic factors could introduce lagged and nonlinear range shifts in response to climate change. At our study site, for example, climate change seems unlikely to result in rapid range contractions in closed canopy forests (due to competitive interactions and slow mortality of existing trees), whereas facilitative interactions at high elevations could enhance range expansions of trees into subalpine meadows. Biotic interactions may therefore cause asymmetric range shift dynamics in response to climate change, especially in the short term.

The strong effects of competition and facilitation, as well as the complex role of origin population found in our study, highlight the multifaceted factors affecting species' ranges. The impacts of these non-climatic factors may interact with climate change in surprising ways, and should not be ignored in forecasts of climate change induced range shifts. For example, biotic interactions

could influence the elevational range shifts of conifers in Mt. Rainier National Park by simultaneously inducing lagged responses (resulting from competitive dynamics) and nonlinear responses (resulting from facilitation) to climate change in the 21st century. These relatively fine scales of space and time (i.e. a single mountain, over the coming decades) are the scales at which natural resource managers typically make decisions, and are therefore critical to managing and mitigating the biological impacts of climate change.

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Data release

The complete dataset is freely available through the Knowledge Network for Biocomplexity (KNB,http://knb.ecoinformatics.org/): *Ailene Ettinger. 2017. Conifer seedling performance on Mt. Rainier. KNB Data Repository. DOI:10.5063/F18C9T6R.*

Figures

Figure 1. Hypotheses. Following classic niche theory, we expected survival and growth to be highest in the middle of the range (a). Furthermore, we hypothesized that if populations are adapted to their local environments, the optimal climate for each population should vary across the range, with peak performance closest to an individual's 'home' environment (b). Given the heavy winter snowpack at Mt. Rainier's high elevations, we hypothesized that climate (specifically snow duration and growing season length) constrains performance at upper range limits of focal species, whereas competition drives performance at lower range limits (c). In other words, we expected that performance would be lower in "high competition" plots at and below lower elevational limits, but that performance would not differ by competitive neighborhood at and above upper limits.

Figure 2. Range position, origin, and competition had complex effects that varied by vital rate and species, shown here by the proportion of variance explained by these predictors**.** Proportion of deviance (from binomial generalized linear mixed-effects models for germination and accelerated failure time models for survival) and variance (from linear mixed-effects models for growth) explained are shown for each explanatory variable and interaction (compared to the total deviance/variance explained in the full model). In this figure, "competition" includes understory, canopy, and their interaction. Models were fit separately for each species and vital rate (see Table 1 for details).

Figure 3. Origin population affected germination (a-c), survival (d-f) & growth (g-i), but effects varied by species. Black circles represent seed originating from lower limit populations (not present for *T. heterophylla*); gray circles represent mid-range populations, and white circles represent upper range limit populations. Mean values are shown across all competition treatments, and error bars represent standard error. Shading shows the elevational range over which the species occurs on the south side of Mt. Rainier.

Figure 4. Competitive treatment affected transplant survival and growth across species' ranges, but not germaination (a-c). The direction of effects varied with elevation: competition from understory (light bars) and canopy (dark bars) negatively affected survival (d-f) and growth (g-i) across most of the ranges for all three species. However, facilitation was evident beyond upper limits, where canopy presence positively affected survival for *T. mertensiana* and *A. amabilis*, and growth of *A. amabilis*. Graphs show effects on germination (a-c), survival time (d-f), and the difference in annual height increment (g-i) in plots with competition present (understory or canopy), relative to those with no above-ground competition (canopy gaps, with understory vegetation removed) at range position, from model estimates fit to our data. We used generalized linear mixed effects models with binomial responses variables for germination, accelerated failure-time models to obtain survival estimates and linear mixed-effects models for height increment estimates, across all origin populations. Interactions between understory and canopy are not shown, as they were small and nonsignificant ($P>0.10$) in all but two cases (survival of *T. heterophylla,* growth of *A. amabilis*). Error bars represent standard error. Shading shows the elevational range over which each species occurs on the south side of Mt. Rainier.

Figure 5. Microclimate varied with competitive neighborhood. The presence of understory and canopy vegetation reduced light levels (a, $P<0.05$, Table 1S); elevation did not have a consistent effect on light (Table 1S). Snow duration (i.e. the number of days with snow present) increased with rising elevation ($P<0.05$) and decreased with canopy presence (b, $P<0.05$, Table 1S). Growing season length (the number of days above 5°C) decreased with rising elevation ($P<0.05$) and increased with

canopy presence at high elevations (c, $P<0.05$). Understory presence had no effect on snow duration ($P=0.24$), nor on growing season length ($P=0.55$). Effects of both types of vegetation are shown, relative to areas with no neighbors (i.e. "effect" is the difference between light levels with neighbors and light levels in canopy gaps with understory removed), as estimated by linear mixed-effects models fit to our 2010-2012 microclimate data (with random effects of block and year); error bars represent standard error ($n=5$ per treatment per elevation).

Supporting Information

Figure 1S. Study sites and experimental design. We established the experiment at seven different elevations on the south side of Mt. Rainier (a, map view). Sites were located in closed canopy forests up to timberline (the upper limit where trees form closed canopy forest), and focal species (*Tsuga heterophylla, Abies amabilis*, and *Tsuga mertensiana*) are dominant climax tree species at lower, mid, and high elevation areas, respectively, on Mt. Rainier. Abundance of adult trees (diameter at breast height greater than 10 cm) observed in 500 m^2 plots is shown (data from Franklin et al., 1988) (b). We transplanted each focal species at five of these elevations: in the middle of its range, at its upper and lower range limits, and beyond the upper and lower ranges (except for *T. heterophylla*, whose lower range limit does not exist in the Park and was transplanted at only three elevations). Each elevation contained transplant plots for two focal tree species, with five blocked replicate plots of each treatment at each elevation. We evaluated differences in canopy competition versus understory competition by establishing plots in areas with forest canopy absent (gaps) and present (non-gaps) at each elevation. Within each canopy type, we established paired 0.25 m^2 plots and removed all aboveground understory vegetation in a half-meter radius around one of the plots in each pair. Panel c shows images from example gaps and nongaps in closed canopy and timberline sites. The top row of images in panel c shows the canopy, with images taken looking up from a height of about 2 meters above the ground surface in the center of the gap or nongap plots. The bottom row of images in panel

c shows the seed addition and transplant plots where understory was removed and where it was left alone, for comparison.

Table 1S. Climate, light, vegetation, and soil characteristics by elevation and canopy status. Mean values, across five replicates at each elevation, are listed. Bolded text indicates significant differences between gaps and non-gaps. Understory presence had a much smaller effect on all microclimate variables, so these values represent means across both understory treatments within each canopy status. (Abbreviations: Elev= Elevation, PAR=Photosynthetic Active Radiation, C=total soil carbon, H= total soil hydrogen, and N= total soil nitrogen).

Table 2S. Effect of moss cover on germination. Model comparisons and coefficients from germination models fit with and without moss cover as a covariate.

Appendix S1. Details of conifer seed storage and propagation methods.

Appendix S2. Statistical methods and results for microclimate models.

Appendix S3. Methods and results for greenhouse germination trials.

Appendix S4. R code for models fit to germination, survival, and transplant data.

Table 1. Analysis of variance table for germination, survival, and growth models summarizes type-III tests for significance. Generalized linear mixed-effects models with binomial response variables were fit for 2011 germination data. Accelerated failure-time models were fit for interval- and right-censored transplant survival data, using a lognormal distribution for failure-time (i.e. lifespan). Linear mixed-effects models, with random effects of block, were fit for average annual height increment (growth) data. Bold text indicates significance (*P*<0.10).

Species	Source	Germination			Survival			Growth		
		χ^2	*df*	*P*	χ^2	*df*	*P*	χ^2	*df*	*P*
Tsuga mertensiana	Intercept	**142.59**	**1**	**<0.01**				**14.55**	**1**	**<0.01**
	Range position	4.99	4	0.29	**10.36**	**4**	**0.03**	**11.78**	**4**	**0.02**
	Origin population	3.38	2	0.18	0.59	2	0.75	**4.64**	**2**	**0.10**
	Canopy	1.50	1	0.22	**17.41**	**1**	**<0.01**	**4.64**	**2**	**0.04**
	Understory	1.19	1	0.27	0.19	1	0.67	**10.34**	**1**	**<0.01**
	Range position *Origin	2.44	8	0.96	**19.74**	**8**	**0.01**	12.29	8	0.14
	Range position *Canopy	1.30	4	0.86	**27.86**	**4**	**<0.01**	6.09	4	0.19
	Range position *Understory	3.98	4	0.41	**20.37**	**4**	**<0.01**	**16.19**	**4**	**<0.01**
	Origin*Canopy	1.08	2	0.58	0.17	2	0.92	4.44	2	0.11
	Origin*Understory	0.01	2	0.99	0.44	2	0.80	0.92	2	0.63
	Canopy*Understory	0.43	1	0.51	0.01	1	0.92	2.44	1	0.12
	Range position *Canopy*Understory	1.17	4	0.88	2.40	4	0.66	**8.91**	**4**	**0.06**
Abies amabilis	Intercept[1]	**60.16**	**1**	**<0.01**				**7.82**	**1**	**<0.01**
	Range position	2.81	4	0.59	**50.49**	**4**	**<0.01**	**70.82**	**4**	**<0.01**
	Origin population	0.04	1	0.84	**10.12**	**3**	**0.02**	2.94	3	0.40
	Canopy	0.00	1	0.97	**11.74**	**1**	**<0.01**	**17.09**	**1**	**<0.01**
	Understory	0.12	1	0.73	**7.92**	**1**	**<0.01**	0.20	1	0.66
	Range position *Origin	**96.64**	**4**	**<0.01**	**23.50**	**12**	**0.02**	18.46	12	**0.10**
	Range position *Canopy	0.43	4	0.8	**127.20**	**4**	**<0.01**	**38.63**	**4**	**<0.01**

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[1] The germination model for this species also includes a covariate of moss: *df*=1, χ^2=3.67 *P*=0.05

	Range position *Understory	0.65	4	0.96	**32.10**	**4**	**<0.01**	**19.81**	**4**	**<0.01**
	Origin*Canopy	1.46	1	0.23	0.51	3	0.92	1.92	3	0.59
	Origin*Understory	0.01	1	0.91	5.46	3	0.14	3.00	3	0.39
	Canopy*Understory	0.13	1	0.72	0.00	1	0.97	0.62	1	0.43
	Range position *Canopy*Understory	0.57	4	0.97	**13.19**	**4**	**0.01**	**11.04**	**4**	**0.03**
Tsuga heterophylla	Intercept[2]	**90.80**	**1**	**<0.01**				**14.50**	**1**	**<0.01**
	Range position	2.16	2	0.34	**23.03**	**2**	**<0.01**	0.19	2	0.91
	Origin population	2.54	1	0.11	2.13	1	0.14	0.05	1	0.82
	Canopy	1.27	1	0.26	**5.43**	**1**	**0.02**	**19.10**	**1**	**<0.01**
	Understory	0.30	1	0.59	**19.26**	**1**	**<0.01**	0.07	1	0.78
	Range position *Origin	1.47	2	0.48	0.41	2	0.81	2.21	2	0.33
	Range position *Canopy	0.76	2	0.68	2.88	2	0.24	1.91	2	0.38
	Range position *Understory	1.30	2	0.52	1.49	2	0.47	2.49	2	0.29
	Origin*Canopy	0.01	1	0.92	1.25	1	0.26	**8.97**	**1**	**<0.01**
	Origin*Understory	0.28	1	0.59	0.77	1	0.38	2.53	1	0.11
	Canopy*Understory	1.88	1	0.17	1.79	1	0.18	0.71	1	0.40
	Range position *Canopy*Understory	0.82	2	0.66	5.45	2	**0.07**	1.70	2	0.43

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[2] The germination model for this species also includes a covariate of moss: df=1, χ^2=8.91 P<0.01

Table 2. Analysis of variance table for microclimate (growing season length, snow duration and light), summarizing type-III tests for significance. Linear mixed-effects models, with random effects of block and year, were fit for growing season length, snow duration (in days), and light (visible light). Bold text indicates significance (*P*<0.10).

Source	x^2	df	P	x^2	df	P	x^2	df	P
Intercept	**1223.43**	**1**	**<0.01**	**50.91**	**1**	**<0.01**	**65.66**	**1**	**<0.01**
Elevation	**896.30**	**6**	**<0.01**	**5094.20**	**6**	**<0.01**	**52.92**	**6**	**<0.01**
Canopy	0.61	1	0.44	**7.30.05**	**1**	**<0.01**	**13.75**	**1**	**0.01**
Understory	1.39	1	0.24	0.98	1	0.32	**5.43**	**1**	**0.02**
Elevation*Canopy	**14.51**	**6**	**0.02**	**12.85**	**6**	**0.05**	7.60	6	0.27
Elevation*Understory	2.35	6	0.88	2.42	6	0.88	**21.28**	**6**	**<0.01**
Canopy*Understory	0.13	1	0.472	0.24	1	0.62	**5.71**	**1**	**0.02**
Elevation*Canopy*Understory	1.79	6	0.94	5.78	6	0.45	7.41	6	0.25

(a) *Niche hypothesis*

(b) *Home-site advantage hypothesis*

Seed origin
- Lower limit
- Mid-range
- Upper limit

(c) *Competition-environmental gradient hypothesis*

Limit determined by competition   Limit determined by climate

Location in range

(a) *Tsuga mertensiana*

Origin*Competition
Elevation*Origin
Elevation*Competi
Origin
Competition
Elevation

Germination   Survival   Growth

(b) *Abies amabilis*

Germination   Survival   Growth

(c) *Tsuga heterophylla*

Germination   Survival   Growth

Vital rate