Testing the Limits: Understanding How Climate and Competition Affect Species' Ranges in a Warming World

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Abstract

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What factors determine where species occur, known as their geographic range limits? This classic ecological question has fascinated scientists for centuries, and is even more relevant today, in the face of anthropogenic climate change. Unfortunately, despite decades of research, we still lack a full understanding of the ecological processes driving range limits. Of particular interest, given forecasted global warming, is the extent to which climate determines species' range limits. If climate is important in controlling species' range limits, then ranges will likely shift up in elevation, as temperatures rise. This research examined how climatic factors, including temperature and precipitation, interact with biotic factors (specifically, competition between plants) to determine the distributions of common conifers on Mt. Rainier. I conducted observational studies of adult and sapling tree rings, as well as an experiment, in which seeds and seedlings were transplanted across species' altitudinal ranges and beyond their range limits, into different competitive environments. Taken together, my studies suggest that climate limits growth and survival at high elevations, while competition is more important at low elevations. These results support a classic, but little tested, hypothesis: biotic factors, such as competition, are more important at lower range limits, while abiotic factors, such as temperature, control upper range limits. Furthermore, these results suggest that climate change will lead to increased tree growth and upward expansion of Mt. Rainier's forests, beyond current high elevation treeline. Climate change will likely have less dramatic effects at low elevations, where climate does not appear to strongly limit growth and survival of focal tree species, but competitive dynamics between plants do limit growth and survival. More experimental studies of other biotic interactions, diverse species, and widespread locations are necessary to better understand effects of climate change, and to prioritize conservation and natural resource management efforts.

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Dedication

This dissertation is dedicated to my mom, Judy Kane, who inspired me to go to graduate school and did not live to see me complete it. She has been and continues to be a great source of strength, wisdom, support, and love, and will forever be remembered for her passion, appreciation, and protection of the natural world, as well as her genuine curiosity, intellect, and generosity.

CHAPTER 1

Ettinger A. K., K. R. Ford, and J. HilleRisLambers. 2011. Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology* 92:1323-1331. doi:10.1890/10-1639.1.

Abstract

Does climate determine species' ranges? Rapid rates of anthropogenic warming make this classic ecological question especially relevant. We ask whether climate controls range limits by quantifying relationships between climatic variables (precipitation, temperature) and tree growth across the altitudinal ranges of six Pacific Northwestern conifers on Mt. Rainier, Washington, USA. Results for three species (*Abies amabilis*, *Callitropsis nootkatensis, Tsuga mertensiana*) whose upper limits occur at treeline (>1600 m) imply climatic controls on upper range limits, with low growth in cold and high snowpack years. Annual growth was synchronized among individuals at upper limits for these high elevation species, further suggesting that stand-level effects such as climate constrain growth more strongly than local processes. By contrast, at lower limits climatic effects on growth were weak for these high elevation species. Growth-climate relationships for three low elevation species (*Pseudotsuga menziesii, Thuja plicata, Tsuga heterophylla*) were not consistent with expectations of climatic controls on upper limits, which are located within closed-canopy forest (<1200 m). Annual growth of these species was poorly synchronized among individuals. Our results suggest that climate controls altitudinal range limits at treeline, while local drivers (perhaps biotic interactions) influence growth in closed-canopy forests. Climate change induced range shifts in closed-canopy forests will therefore be difficult to accurately predict.

Introduction

Climate has long been thought to play a dominant role in controlling species' range limits (Darwin 1859, Grinnell 1917, MacArthur 1972). In support of this idea, species distributions often correspond to thermal isoclines (Sorenson et al. 1998, Buckley et al. 2010). Also, species' range shifts during the Holocene, preserved in macrofossil and pollen records, have tracked climatic changes (e.g. Prentice et al. 1991, Davis and Shaw 2001). Finally, many species have moved to higher latitudes and altitudes with warming during the last century (Parmesan 2006).

Despite these compelling links between climate and species' distributions, the role climate plays in determining range limits is still not fully understood. Species' responses to recent warming are inconsistent: although some ranges have moved upwards or polewards as expected, others remain static or have shifted in the opposite direction from that expected (e.g. Parmesan 2006, Harsch et al. 2009). This suggests that controls on range limits may not always be climatic. Biotic interactions like competition and facilitation are also known to influence species distributions (e.g. Connell 1961, Brown et al. 1996), and could be more important than climate for some species or locations, perhaps explaining the inconsistent responses to recent warming. Unfortunately, little is known about the influence of biotic interactions on range limits (Sexton et al. 2009). Consequently, forecasts of global warming-induced changes in species distributions often assume climate is the sole driver of range limits (Pearson and Dawson 2003).

Understanding effects of climate change on tree ranges is particularly important, as forests provide important ecosystem services (e.g. carbon sequestration). Trees also offer valuable opportunities for studying climatic controls on range limits because annual rings preserve growth-climate relationships across many years (e.g. Peterson and Peterson 2001, Littell et al. 2008, Chen et al 2010). The role of biotic factors in limiting tree distributions remains poorly understood, in part because tree rings are generally sampled from extreme environments where competition is low, in order to maximize the climate signal (Stokes and Smiley 1968). While useful for reconstructing past climate, this approach probably will not give an accurate picture of how trees in closed-canopy forests respond to changes in climate.

To address these issues, we examined growth-climate relationships for six conifer species with contrasting altitudinal ranges on Mt. Rainier (Fig. 1). We collected 90+ years of annual tree growth data from over 600 individual trees growing at nine different elevations on Mt. Rainier, where long-term climate records exist. We used this extensive dataset to ask i) whether the relationship between growth and climate suggests climatic controls on upper and lower range limits of focal conifers; and ii) how the relative importance of stand-level drivers (e.g. climate) vs. localized drivers (e.g. biotic interactions) of growth varies across altitudinal ranges. If climate controls altitudinal range limits, we hypothesized that growth would be strongly influenced by climate at range limits, with the sign of these relationships or identity of important climatic drivers differing between upper and lower range limits (Fig. 1A&B). There are strong elevational gradients in climate on Mt. Rainier (Fig. 1C&D), and precipitation consists mainly of winter snowfall, so heavy precipitation reduces the length of the growing season. We therefore expected that temperature would positively influence growth at upper limits and negatively influence growth at lower limits, and that precipitation would negatively influence growth at upper limits and positively influence growth at lower limits, if climate controls range limits. We were also interested in how focal species differ in the identity of the climate variables influencing growth. Finally, we expected growth to be highly synchronized among conspecific individuals at range limits if climate is an important driver; that is, a "good" growth year should be good for all trees in a stand. By contrast, if biotic factors drive altitudinal range limits, we expected annual growth trends to be asynchronous among individuals.

Methods

Study site & species

We collected data in Mt. Rainier National Park, located in the western Cascade Mountains of Washington state. Mt. Rainier is a 4,392-meter high volcano that has remained relatively undisturbed since its creation as a park in 1899. Soils are podzolic, with surface organic horizons that have accumulated over soil horizons buried from multiple volcanic ash deposits (Franklin et al 1988). The climate is temperate maritime, with dry summers, heavy winter precipitation, and strong elevational gradients in climate (Fig. 1C&D).

We sampled six conifer species that are dominant on Mt. Rainier's south side (Fig. 1B) and abundant in western Washington (Franklin et al. 1988, Burns and Honkala 1990). This included three high elevation species (*Abies amabilis* Douglas ex J. Forbes [Pacific silver fir], *Callitropsis nootkatensis* (D. Don) Florin ex D. P. Little [formerly *Chamaecyparis nootkatensis*, Alaskan yellow-cedar], and *Tsuga mertensiana* (Bong.) Carrière [mountain hemlock]), whose upper range limits extend to treeline (>1600 m). We also sampled three low elevation species (*Pseudotsuga menziesii* (Mirb.) Franco [Douglas-fir], *Thuja plicata* (Raf.) Sarg. [western red-cedar], and *Tsuga heterophylla* (Raf.) Sarg. [western hemlock]), whose upper range limits occur in closed canopy forests (< 1200 m). Sampling locations included upper altitudinal range limits of all focal species and lower limits of the high elevation species (Fig. 1B) (Franklin et al. 1988).

Tree growth data

We collected increment cores from 20 individuals per focal species at nine elevations spanning closed-canopy forests to treeline (704-1603 m in altitude). We cored trees adjacent to nine one-hectare permanent study stands established in the 1970s as part of a Permanent Sample Plot Network (Dyrness and Acker 2000). Cored trees were greater than 40 cm in diameter at breast height and located at least 20 m apart. We collected two cores per individual on opposite sides of the tree, perpendicular to the aspect. Increment cores were sanded, and then scanned with a high-resolution scanner using the program WinDendro (Version 2008e) to measure annual growth rings to 0.001 mm (Regent Instruments, Inc). We used visual cross-dating to identify missing and false rings and to date annual rings to the calendar year (Stokes and Smiley 1968). We verified the accuracy of visual cross-dating with the Dendrochronology Program Library (dplR) package in R, Version 2.10.1 (R Development Core Team 2009, Bunn 2010). The sample size was reduced to 19 individuals for one species-stand combination, *T. mertensiana* at 1197 m, where cores from one tree were discarded due to rot.

We averaged ring widths from the two collected cores for each individual tree, then standardized each tree's ring width series by fitting a spline through the time series to remove size-specific trends (Cook and Peters 1981). We set the spline's rigidity at 100 years and its wavelength cutoff at 50% (e.g. Nakawatase and Peterson 2006, Littell et al. 2008). More- or less-flexible splines did not qualitatively influence our results. After splining, dimensionless ring-width indices (RWI) were used as a measure of annual tree growth.

Climate data

Climate records (1914-2007) came from the Longmire Ranger Station at 842 m, located within our altitudinal transect (http://lwf.ncdc.noaa.gov/oa/climate/climatedata.html). Longmire climate is strongly correlated with climate directly above (Paradise Ranger Station, 1654 m) and below (LaGrande, 293 m) our sampling locations (Fig. 1S, supplemental information). We chose nine climate variables as potential explanatory variables in our analyses: mean annual temperature (MAT), mean growing season temperature (GST, May to September), mean dormant season temperature (DST, November to March), total annual precipitation (PPT), total growing season precipitation (GPT), total dormant season precipitation (DPT), maximum size of the snowpack in snow water equivalent (SWE), snow duration (SNDR, the number of days the ground was covered by snow in a given year), and growing degree days (GDD, the annual sum of daily mean temperatures for days with mean temperatures above 5°C). All annual variables were calculated for hydrologic years, from October to September. Tree growth is also influenced by potential evapotranspiration in the Pacific Northwest (PET - e.g. Littell et al. 2008); however, we did not include PET as an explanatory variable because data are available on much shorter time scales than temperature and precipitation. Moreover, PET is highly correlated with the climatic variables we did include (Fig. 2S).

We combined climate data from Longmire with output from a climate-mapping model called PRISM (Parameter-elevation Regressions on Independent Slopes Model) to estimate a climatic time series at each of our sampling locations. PRISM uses climate station data, digital elevation models, and physiographic-climate relationships to estimate temperature and precipitation on a 30-arcsec (~800 m) grid (Daly et al. 2008). We used climate estimates for the grid cells within which sampling locations were located to create a 1914-2007 time series for each climate variable at each sampling location (Supplemental Methods).

Statistical Analyses

Growth-climate relationships: We used linear mixed-effects models to evaluate the relationship between growth and climate for each species at each sampling location. Unlike most standard dendroecological analyses (where analyses are based on average RWIs of all individual trees at a site), mixed-effects models allowed us to accommodate differences among individual tree responses to climate. We designated both individual tree and year as random effects to account for non-independence of data from the same individual or within years (Crawley 2007); all climate variables were fixed effects. We used the lme4 package in R for fitting mixed-effects models (R Development Core Team 2009, Bates and Maechler 2010).

To evaluate which combination of climate variables (if any) best explained annual growth patterns, we fit 32 linear mixed-effects models for each species at each sampling elevation using maximum likelihood estimates. Our models ranged from a null (only an intercept) and all single climate variable models (models with only mean annual temperature, only growing season precipitation, etc.) to more complicated models with two-way interactions between climate variables (see Supplemental Methods for a list of models). The 32 models we fit constitute only a subset of all possible models; we excluded models with highly correlated explanatory variables ($r>0.6$, e.g. mean annual temperature and dormant season temperature, Fig.2S&3S) and what we viewed as biologically implausible combinations of explanatory variables (e.g. three-way interactions). We standardized climate variables by subtracting the mean and dividing by the standard deviation to facilitate direct comparison of climate coefficients from different explanatory variables. We used Akaike's Information Criterion (AIC) to identify the 'best-fitting' model for each species at each sampling elevation, choosing the model with the fewest parameters when AIC values of the best-fitting and next best-fitting model(s) differed by less than 2.0 units (Burnham and Anderson 2002). We also used the difference in AIC values between the null model and the best-fit model to indicate the extent to which climate explains variation in observed tree growth (AIC_{Null}-AIC_{Best}). We calculated significance of coefficients using the LanguageR package in R, which estimates *P*-values using Markov chain Monte Carlo (MCMC) sampling (Baayen et al 2008). We also applied linear regressions to the growth of each individual tree to determine the proportion of trees sensitive to climate at each elevation. These linear models included climate variables identified in the best-fit mixed-effects model. We considered an individual tree sensitive to climate if climate explanatory variables were significant ($P<0.05$) in the linear regressions.

Synchronized growth: We assessed the importance of stand-level effects versus localized factors by calculating all pair-wise correlations (Pearson's *r*) between the RWIs of all individual conspecific trees within each sampling location, and then averaging correlation coefficients per species and sampling location. This single measure of growth synchrony allowed us to contrast the importance of stand-level processes for annual growth at different elevations. We assumed that a high degree of growth synchrony, as indicated by high tree-to-tree correlations, implies that stand-level processes like climate influence growth, while low synchrony, indicated by low correlations, suggests local drivers like biotic interactions.

Results

The strength of growth-climate relationships and the identity of climatic variables in best-fit models differed by elevation and by tree species (Table 1, Fig. 2&3). For example, snowpack was inversely related to *C. nootkatensis* growth at the three highest elevations, influencing between 45% and 95% of individual trees. However, growing degree days alone best explained growth at the lowest elevation where this species occurred, but only 35% of individuals were influenced by this climate variable (Table 1). In contrast, growing degree days had minimal influence on the growth of *T. heterophylla*; instead, growing season temperature was important at three of the seven locations for this species, and it was negatively related to growth in all cases. *T. heterophylla* was less sensitive to climate than the other five species, with fewer than 20% of individuals sensitive to climate at all but one location (Table 1, Fig. 2).

In the three high elevation species, growth-climate relationships were consistent with expected relationships for climatic drivers on upper range limits (Table 1, Fig. 3). For example, our data suggests that *A. amabilis* growth was negatively affected by snowpack, which increases with elevation, at its upper range limit (Table 1). Climate sensitivity was greatest at higher elevations (i.e. upper limits), as indicated by the large size of climate coefficients and large AIC_{Null}-AIC_{Best} values (ranging from 67 to 70) for these species. Additionally, populations of high elevation species were consistently sensitive to climate (90-100% of trees) at upper range limits, where individual trees also showed synchronized growth, suggesting stand-level drivers (like climate) of performance.

In contrast, at the lower range limits of high elevation species, climate coefficients and AIC_{Null}-AIC_{Best} values (ranging from 15 to 28) were lower relative to upper range limits. Additionally, the sign of climate variable coefficients was not consistent with expectations of climatic controls on lower range limits (Fig. 1). Growth of *C. nootkatensis,* for example, was positively related to growing degree days at its lower limit, even though values of growing degree days decrease with elevation (Table 1). Furthermore, fewer individual trees were sensitive to climate at lower than upper range limits (25%, 35% and 53% for *A. amabilis, C. nootkatensis,* and *T. mertensiana*). Finally, growth was much less synchronized among individual trees at lower range limits, suggesting localized drivers of growth at lower limits (Table 1).

Growth-climate associations for the three low elevation species (*P. menziesii, T. plicata*, and *T. heterophylla*) were not consistent with expectations of climatic drivers on their upper altitudinal range limits. Climatic effects on these species' growth were weaker than for the high elevation species, as indicated by lower values of AIC_{Null}-AIC_{Best} and lower coefficients (Table 1, Fig. 3). Second, even when AIC_{Null}-AIC_{Best} values increased with elevation (e.g. *P. menziesii*, Table 1), as expected if climate determines upper range limits, the proportion of individuals sensitive to climate and growth synchrony was low compared to high elevation species (Fig. 3). Furthermore, the sign of climate coefficients was generally inconsistent with expectations for climatic controls on range limits for low elevation species. For example, our results suggest that at the upper range limit of *T. heterophylla*, snow had a nonsignificant positive effect on growth; however, if snowpack limits growth, it should negatively affect growth at upper range limits.

Discussion

Our results suggest that climate drives some, but not all, range limits. Annual growth of high elevation conifers declines with high levels of snow, low growing season temperatures or low growing degree days at upper range limits (Table 1, Fig. 2). This likely reflects constraints on the tree life-form or species-specific physiological tolerances. Other studies have found that snowpack limits growth and prevents tree expansion into Pacific Northwestern subalpine meadows (Taylor 1995, Nakawatase and Peterson 2006), and temperature is thought to strongly control treeline across the globe (Körner and Paulsen 2004). Growth-climate relationships of high elevation species did not support climatic controls on lower range limits, however. Annual growth was less sensitive to climate in lower- versus upper- elevation populations, and the identities and signs of climatic drivers were similar across lower and upper range limits for individual species, contrary to expectations if climate determines lower range limits (Fig. 1A).

Additionally, growth of the low elevation species was not strongly limited by climatic variables at upper altitudinal range limits, nor was the sign of climate coefficients consistent with climatic drivers on range limits (Table 1). Climate may play a more important role in determining range limits of these species elsewhere. For example, Littell et al. (2008) found that *P. menziesii* is negatively influenced by summer water deficit in populations east of our study area that experience much drier conditions. Alternatively, populations in different regions may have adapted to local environments and respond differently to climate (Chen et al 2010).

If climate does not control tree growth at all range limits of our focal species, what does? Localized drivers, not climate, appear to be responsible. The extent to which growth is synchronized among individuals across altitudinal ranges mirrors growth-climate relationships for the three high elevation species, with greatest synchrony and strongest growth-climate relationships at upper range limits (Table 1, Fig. 3). This suggests that when climate limits growth, it does so consistently for all individuals. For low elevation species, growth synchrony between individuals did not vary consistently across altitude and growth-climate relationships were weak (Table 1, Fig. 3). Thus, where climate effects are weak, factors in the local neighborhood of individual trees appear to drive growth. Other studies have also found that tree growth is buffered from regional climate by local conditions (e.g. Holman and Peterson 2006).

Local drivers of tree growth at range limits where climate does not play a strong role may reflect biotic interactions such as competition and facilitation. Studies suggest that the importance of biotic interactions increases as abiotic conditions become less stressful (Brown et al 1996, Menge and Sutherland 1987), i.e. with decreasing elevation (Fig. 1). Indeed, tree range limits may be influenced by biotic interactions, such as interspecific competition (Armand 1992, Loehle 1998, Price and Kitckpatrick 2009). Facilitation is also known to affect plant distributions (e.g. Choler et al 2001), and may also play a role at Mt. Rainier. We did not explicitly examine biotic factors, and believe that the exact biotic drivers of focal species range limits (if any) deserve further study.

It is also possible that climatic constraints on range limits occur at other life history stages, as species differ in sensitivity to climate across life stages (Garcia et al. 2000, Bansal and Germino 2010). For example, focal species may be more climatically sensitive as juveniles, as the well-developed root systems of adults can better withstand severe conditions, such as freezing or low moisture, than seedlings (Mote et al. 2003). However, increased annual growth for adult trees corresponds to increased fitness in conifers (e.g. Despland and Houle 1997), and mortality of most trees follows years of low growth (Wyckoff and Clark 2002). Thus, we believe that the strength and direction of growth-climate relationships for adults (as in Fig. 1A) are a good indication of how and whether climate determines population persistence at range limits.

Our results imply that climate change impacts on Pacific Northwestern forests will be difficult to accurately predict using climate envelope models (e.g. Hannah et al 2007), which assume that all range limits are determined by climate (Pearson and Dawson 2003). Average temperatures are expected to increase 3°C by the 2080s, with strongly declining snowpack (Mote and Salathé 2009). Although high elevation species will likely show increased growth at treeline in response to these changes (Table 1, Salzer et al. 2009), responses at lower altitudinal range limits will be more idiosyncratic. For example, if summer precipitation decreases, as forecasted (Mote and Salathé 2009), *T. plicata* growth rates may decline at their upper range limit (where growing season precipitation positively influenced growth, Table 1). Contrary to expectations under climate warming, this could lead to upper range limit contractions in this species at Mt. Rainier. Additionally, where climate does not determine range limits at all (e.g. upper limit of *T.*

heterophylla, Table 1), species' ranges should remain static or shift for reasons not related to climate change (as has been seen in some recent studies, e.g. Harsch et al. 2009).

Conclusions

Despite decades of ecological research, the role of climate in determining species' ranges remains poorly understood. We applied sophisticated analyses to extensive data and show that, contrary to common assumptions, climate does not determine all range limits. Climate strongly constrains performance at upper limits of conifer species reaching treeline, but more localized processes drive growth at upper range limits within closed-canopy forests. We suggest that biotic interactions are likely to be strong in closed canopy forests, and may constrain performance more than climate (Menge and Sutherland 1987). The distribution of Pacific Northwestern conifers may therefore conform to the hypothesis that physiological tolerance limits species distributions where climate is harsh, but biotic interactions affect distributions where climate is not stressful (e.g. Brown et al 1996). The lack of climatic constraints on all range limits suggests that range shifts in a time of climate change will be difficult to accurately predict, particularly in closed-canopy forests where biotic interactions may be important range determinants.

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Table 1. Climate sensitivity across focal tree species' ranges. Climate determines some, but not all, range limits in focal species, based on best-fit models, climate coefficients, comparison of coefficients with Hc (hypothesized sign of climate coefficients if climate drives range limits; Fig. 1), the strength of climatic influence on growth (AIC_{Null}-AIC_{Best}), the proportion of trees sensitive to climate, and synchrony (the degree to which individual tree growth was correlated within a stand; Pearson's *r*). Text is bold if results match Hc at range limits. Climate variables are standardized, so coefficients are directly comparable. * indicates significant effects of coefficients ($P<0.05$), based on MCMC sampling (see text).

					Temperature variables		**Precipitation variables**					
	Species	**Elev (m)**	**Location in Range**	**Best-Fit Model**	**Growing Season**[a]	**Dormant Season**[b]	**Growing Season**[c]	**Dormant Season**[d]	**Do coefficients match Hc at range limits?**	**AIC_{Null} - AIC_{Best}**	**Proportion trees sensitive**	**Synchrony (mean *r*)**
Low elevation Species	*Pseudotsuga menziesii*	704	Mid	DST		0.0306*				4	0.32	0.25
		851	Mid	GDD	-0.0137					9	0.10	0.31
		950	Mid	DST		0.0123				9	0.15	0.34
		1064	Mid	SNDR				0.0067		16	0.20	0.30
		1091	Upper limit	GDD + SWE	-0.0002			0.0251	No	15	0.24	**0.41**
	Thuja plicata	704	Mid	SNDR				-0.0628*		43	0.21	0.26
		851	Mid	SWE				-0.0068		8	0.25	0.19
		950	Mid	Null						0	NA	0.31
		1064	Mid	GDD + GPT + DPT	0.0312*		0.0402*	-0.0440*		17	0.50	0.34
		1091	Upper limit	GDD + GPT	0.0158		0.0301*		No	7	0.27	0.30
	Tsuga heterophylla	704	Mid	SWE				-0.0032		7	0.10	0.19
		851	Mid	GST + DST	-0.0304*	0.0290*				10	0.20	0.13
		950	Mid	GST	-0.0229*					3	0.10	0.14
		1064	Mid	SNDR				-0.0024		9	0.15	0.18
		1091	Mid	GST + SNDR	-0.0441*			-0.0526*		23	0.60	0.38
		1197	Upper limit	SWE				0.0091	No	4	0.15	0.24
High elevation Species	*Abies amabilis*	704	Lower limit	SWE				-0.0058	No	18	0.25	0.07
		950	Mid	Null						0	NA	0.23
		1064	Mid	Null						0	NA	0.33
		1197	Mid	GDD + DST + GPT + DPT	0.0298	-0.0206	0.0372*	-0.0309		18	0.35	0.34
		1454	Mid	SWE				-0.0534*		20	0.45	0.41
		1460	Mid	GDD+SWE	0.0058			-0.0851*		69	0.74	0.38
		1603	Upper limit	SWE				**-0.1338***	**Yes**	**70**	**1.00**	**0.59**
	Callitropsis nootkatensis	1197	Lower limit	GDD	0.0506*				No			
		1454	Mid	GST + SWE	0.0106			-0.0530*				
		1460	Mid	GST + GPT + SWE	0.0455*		0.0483*	-0.0480*				
		1603	Upper limit	GDD + SWE	**0.0342***			**-0.1107***	**Yes**			
	Tsuga mertensiana	1197	Lower limit	GDD	0.0363*				No	27	0.53	0.12
		1454	Mid	GDD + SWE	0.0443*			0.0247		26	0.55	0.21
		1460	Mid	GDD	0.0557*					21	0.50	0.25
		1603	Upper limit	GDD + SWE	**0.0405***			**-0.0734***	**Yes**	**69**	**0.90**	**0.31**

[a] *mean growing season temperature (GST) and growing degree days (GDD)*

[b] *mean dormant season temperature (DST) and mean annual temperature (MAT)*

[c] *total growing season precipitation (GPT)*

[d] *total dormant season precipitation (DPT), snow water equivalent (SWE) and snow duration (SNDR)*

Figure Legends

Figure 1. Climate and species' ranges. If climate controls altitudinal range limits, we hypothesize that growth is strongly influenced by climatic variables at upper and lower range limits, with the direction of these relationships or identity of the climatic driver (temperature [temp] or precipitation [precip]) differing between upper and lower range limits (A). Hc is the hypothesized direction of influence of climatic drivers on growth, if climate drives range limits. Climatic drivers could be annual or seasonal (dormant vs. growing). We examined growth-climate relationships in six tree species with different altitudinal ranges (B): *Abies amabilis* (Abam), *Callitropsis nootkatensis* (Cano), and *Tsuga mertensiana* (Tsme), occurring at high elevations; *Tsuga heterophylla* (Tshe), *Pseudotsuga menziesii* (Psme), and *Thuja plicata* (Thpl) at low elevations. Solid lines indicate >30% probability of occurrence; dashed lines indicate <5% (data from Franklin et al 1988); gray shading is the range of sampling elevations. Mean annual temperature (C) and other temperature-related variables decrease with elevation, while total annual precipitation (D) and precipitation related variables increase with elevation.

Figure 2. Climate determines some, but not all, range limits in focal species. Annual growth (measured by mean ring width index, RWI) of high elevation conifers, such as *Callitropsis nootkatensis* (shown), was inversely related to snow water equivalent (SWE, standardized) at upper range limits (A). The effect of SWE on growth was weaker at the lower range limit (B) and the sign of the effect of SWE on growth was not consistent with climatic controls on the lower range limit (see Fig. 1A). Growth in low elevation conifers, including *Tsuga heterophylla* (shown), was poorly explained by climate variables, such as SWE, at its upper range limit (C) and mid-range (D). (The lower limit does not occur for this species in Mt. Rainier National Park.) See Table 1 for results from all specie

Figure 3. Climatic effects on growth are stronger in high elevation species vs. low elevation species. The strength of climatic effects on model fit (AIC_{Null}-AIC_{Best}; A,B), proportion of individual trees sensitive to climate (C,D), and growth synchrony (E,F) are shown for the six focal species across their altitudinal ranges. Low elevation species, whose upper limits occur in closed-canopy forests, do not show consistent altitudinal trends for changes in model fit with the addition of climate (A), proportion of sensitive trees (C), or growth synchrony (E). In contrast, climate increases model fit at upper range limits (B), with the proportion of individual trees sensitive to climate (D), and synchrony (F) increasing with elevation for high elevation species.

Figures

Figure 1.

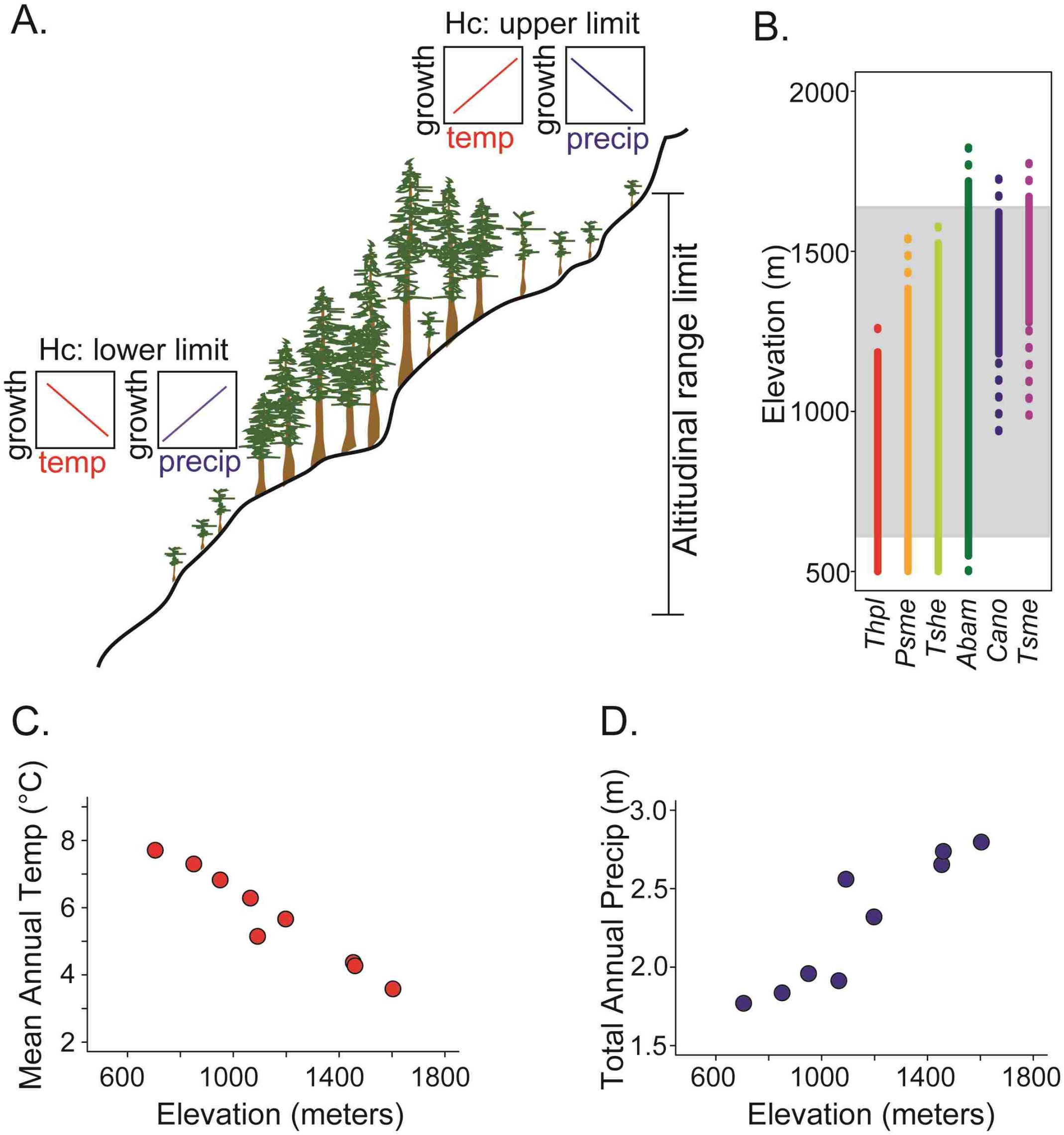


Figure 2.

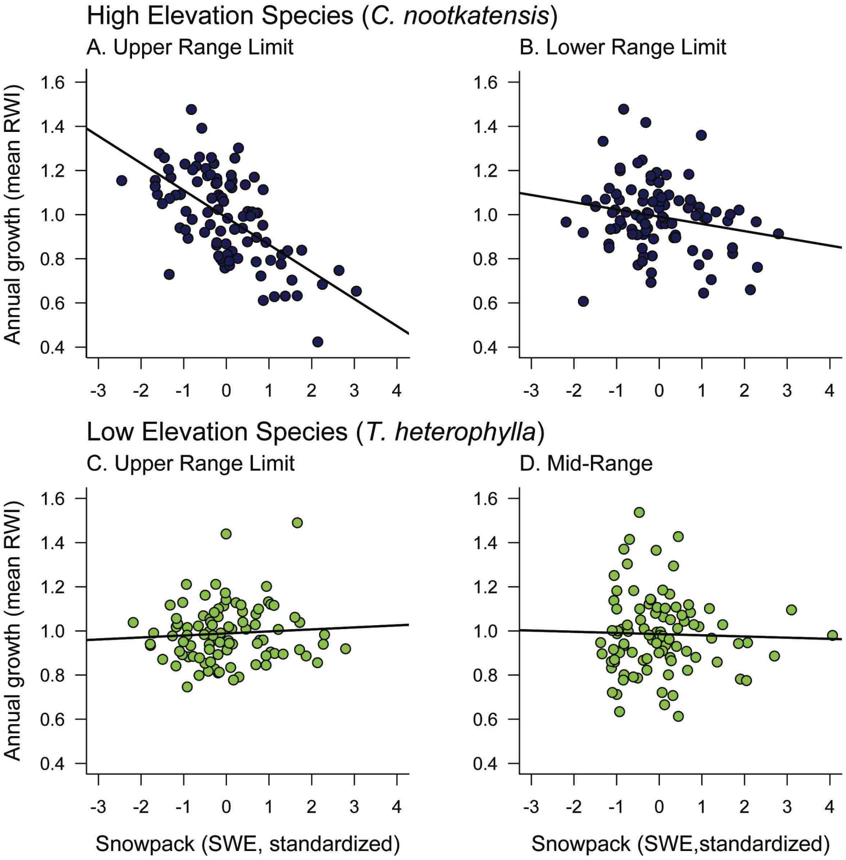
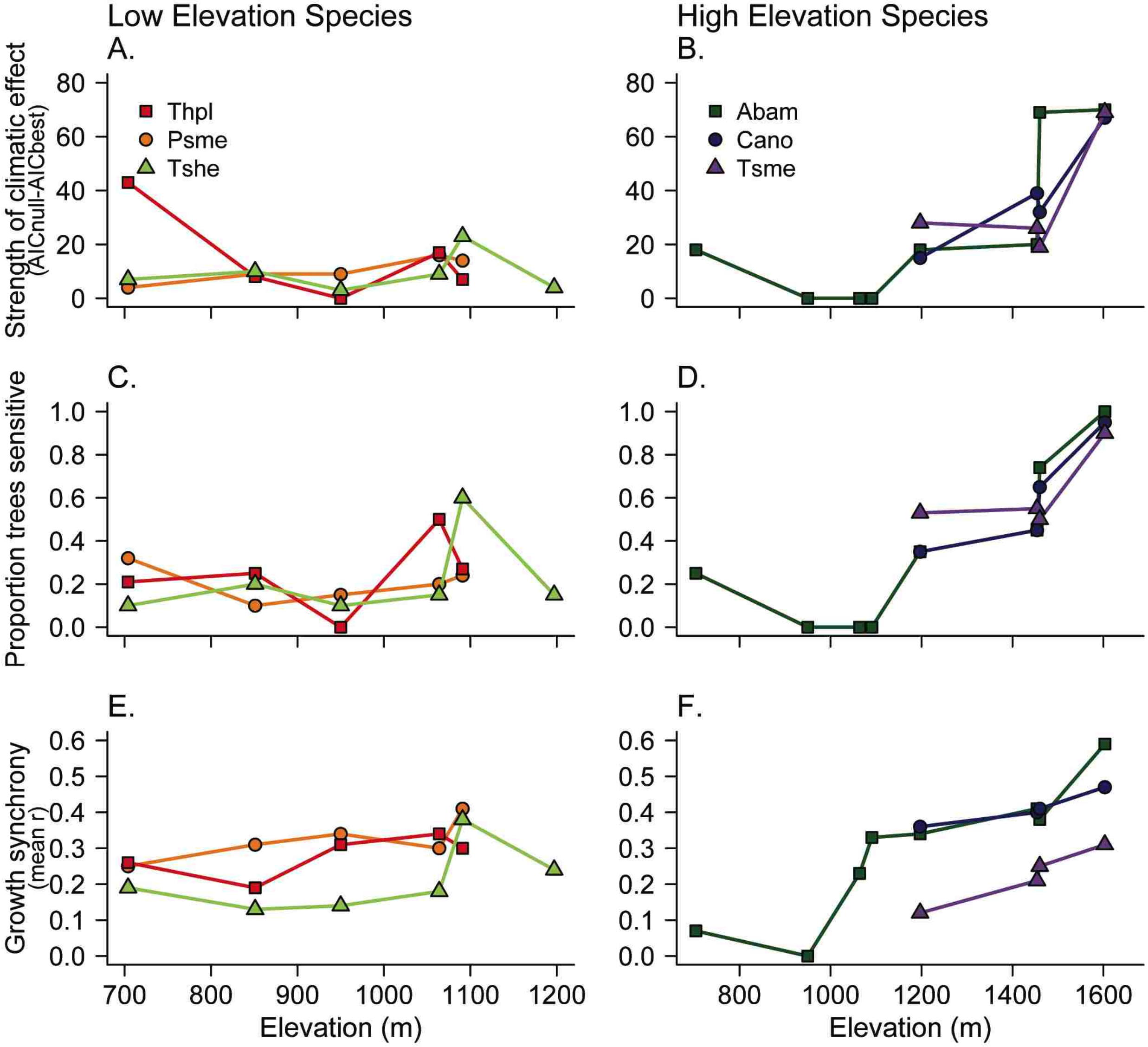

High Elevation Species (*C. nootkatensis*)
A. Upper Range Limit
B. Lower Range Limit
Low Elevation Species (*T. heterophylla*)
C. Upper Range Limit
D. Mid-Range
Annual growth (mean RWI)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
-3
-2
-1
0
1
2
3
4
Snowpack (SWE, standardized)
Snowpack (SWE,standardized)

Figure 3.


Low Elevation Species
High Elevation Species
A.
B.
C.
D.
E.
F.
Strength of climatic effect (AICnull-AICbest)
Proportion trees sensitive
Growth synchrony (mean r)
Thpl
Psme
Tshe
Abam
Cano
Tsme
0
20
40
60
80
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
700
800
900
1000
1100
1200
1400
1600
Elevation (m)

CHAPTER 2

Ettinger A. K. and J. HilleRisLambers. 2013. Climate isn't everything: competitive interactions and variation by life stage will also affect range shifts in a warming world. *American Journal of Botany* 100(7): 1344–1355. doi:10.3732/ajb.1200489.

Abstract

The extent to which climate controls species' range limits is a classic biological question that is particularly relevant given anthropogenic climate change. While climate is known to play a role in species distributions, biotic interactions such as competition also affect range limits. Furthermore, climatic and biotic controls of ranges may vary in strength across life stages, implying complex range shift dynamics with climate change. We quantified climatic and competitive influences on growth of juvenile and adult trees of three conifer species on Mt. Rainier, Washington, United States. We collected annual growth data of these trees, which we compared to the competitive environment and annual climate (100 yr of data) experienced by each individual. We found that the relationships between growth and climate and between growth and competition differed by life stage and location. Growth was sensitive to heavy snowpack and cold temperatures at high elevation upper limits (treeline), but growth was poorly explained by climate in low elevation closed-canopy forests. Competitive effects on growth were more important for saplings than adults, but did not become more important at either upper or lower range limits. In all, our results suggest that range shifts under climate change will differ at leading vs. trailing edges. At treeline, warmer temperatures will lead to increased growth and likely to range expansion. However, climate change will have less dramatic effects in low elevation closed-canopy forest communities, where growth is less strongly limited by climate, especially at young life stages.

Introduction

Understanding the extent to which climate determines species' range limits has become a pressing question in biology, given anthropogenic climate change and its potential effects on natural resources (Thomas and Lennon 1999; Colwell et al., 2008; Lawler et al., 2010; Summers et al., 2012). A species' range is essentially the spatial representation of its ecological niche (Brown et al., 1996), or the "narrow range of environmental conditions" tolerated by a species (Grinnell, 1917). Climate is thought to play a dominant role in controlling species' range limits (Darwin, 1859; Grinnell, 1917; MacArthur, 1972), and there is substantial evidence in support of this idea. For example, species' range shifts during the Holocene as preserved in macrofossil and pollen records have tracked broad climatic changes (Prentice et al., 1991; Davis and Shaw, 2001). Furthermore, over the past 100 years many species have moved to higher latitudes and elevations, presumably in response to recent warming (e.g. Parmesan, 2006; Chen et al., 2011). As a result, the magnitude of range shifts in response to particular warming scenarios are often predicted using the correlation between species' current ranges and current climate, under the assumption that species distributions will shift in sync with future warming scenarios (Fig. 1).

However, nonclimatic factors, such as biotic interactions, dispersal limitation, and evolutionary constraints also play a role in determining species ranges (Grinnell, 1917;

Connell, 1961; Loehle, 1998; Emery et al., 2001; Sexton et al., 2011). Biotic interactions in particular have the potential to lead to unexpected range shift dynamics as temperatures warm (Doak and Morris, 2010). For example, the lower range limits of intertidal prey species (acorn barnacles) did not shift downward to cooler and wetter microclimates as expected with 50 years of warming because of the presence of an important predator in the lower intertidal (Harley, 2011). Additionally, the distribution of a butterfly in England rapidly moved northward once it changed host preference to a different, more northerly distributed plant species (Pateman et al., 2012). Experimental studies, such as with California grassland plants (Suttle et al., 2007), also demonstrate that species interactions can override the direct responses of species to changing climatic factors, suggesting that biotic factors may play a dominant role in climate change responses. These studies exemplify why relying exclusively on climatic factors to forecast species shifts under global warming (i.e., the correlative "bioclimate envelope") has been criticized for its omission of biotic interactions (Davis et al., 1998; Pearson and Dawson, 2003).

Responses to climate change may be further complicated if there is variation in sensitivity to climatic and biotic factors across life history stages (Russell et al., 2012). Such complications are particularly likely for long-lived, sessile species, including some corals, perennial plants, and trees (e.g., Garcia et al., 2000; Bansal and Germino, 2010; Doak and Morris, 2010). For example, the well-developed root systems of adult trees may better withstand severe climatic conditions, such as freezing or low moisture, than seedlings (Mote et al., 2003). Strong effects of competition and gap dynamics have also been documented on tree establishment, growth, and distributions (e.g., Harmon and Franklin, 1989; Gray and Spies, 1997; He and Duncan, 2000), and seedlings may be more sensitive to overstory competition than adult trees (Lusk and Smith, 1998). Such differences among life stages in sensitivity to climate or biotic interactions may have dramatic consequences for future species' ranges, by causing warming-induced range expansion or contraction (or both) to lag behind climate change (Jackson et al., 2009; McLaughlin and Zavaleta, 2012; Zhu et al., 2012). Current forecasting tools may not capture this complexity because most climate change forecasting models are parameterized with a single life stage, generally adults (e.g., Sykes et al., 1996; Chen et al., 2010).

To better understand the potential complexity of range limit dynamics, we examined the influence of climate and competitive environment (i.e., trees in close proximity that may compete for light or other resources) on growth of juvenile (saplings, 1–2 m in height) and adult trees (>40 cm in diameter at breast height) of three conifer species across their elevational ranges. We did this by quantifying annual growth (using ring widths) for trees and saplings of three species at seven locations spanning a 900-m elevational gradient on Mt. Rainier, Washington, United States (Appendix S1). This gradient included the upper range limits of all three focal species and lower range limits of two species. Growth histories were then compared with a 90-year time series of climate (e.g., temperature, snow) and the current competitive environment to determine the influence of climate and competition on performance. We used these data to determine (1) if growth is influenced primarily by climate, competitive environment, or both; (2) how the effect of these factors differed at upper vs. lower range limits and whether the direction of these effects suggested controls over upper and lower range limits of focal conifers; and (3) whether the influence of climate and/or competition on growth at range limits differed by life history stage (Fig. 2).

Previous research suggests that trees often experience strong climatic controls over their upper latitudinal and elevational range limits, but not their lower limits (e.g., Brown et al., 1996; Loehle, 1998; Nakawatase and Peterson, 2006; Ettinger et al., 2011). We therefore hypothesized that climate constrains growth at high elevations (upper range limits of our two high elevation focal species), whereas competitive interactions limits growth at lower range limits in closed-canopy forests (Fig. 1, Appendix S1; Ettinger et al., 2011), where dense tree crowns fill the canopy layer and little light reaches the forest floor directly. Thus, we expected the magnitude and direction of climatic and competitive effects on growth to vary by range position. Specifically, given climate–elevation patterns at Mt. Rainier (i.e., decreases in temperature and increases in snow with rising elevation), we expected that temperature would positively influence growth and winter snow would negatively influence growth at upper limits (Fig. 2), but have little effect on growth at lower range limits. By contrast, we expected that growth would be most depressed by high competitive environments at lower range limits (Fig. 2).

We also expected that competitive interactions would influence juvenile tree growth more strongly than for adult trees (Fig. 2) because of severe competition for light under dense forest canopies. We were not certain how juvenile trees would differ from adult trees in their climate sensitivity because there is competing evidence about whether juveniles should show similar, more, or less climate sensitivity than adult trees. On the one hand, juveniles often tolerate narrower environmental conditions than adults (Jackson et al., 2009). Furthermore, substantial winter snowpack and low summer precipitation play large roles in the Pacific Northwest forests where we conducted this study (Franklin et al., 1988; Mote et al., 2003; Ettinger et al., 2011). Juvenile trees, with their shorter stature and less-developed root systems, could be more sensitive to these climatic constraints than adults. Alternatively, competition for light may be so limiting that only adult trees reaching the upper canopy (and leaving light competition behind) show growth responses to climate.

Materials and Methods

To understand the roles of climate and competition in determining range limits, we quantified their influences on growth of juvenile and adult trees of three conifer species. We collected data on annual growth of trees and saplings, which we compared to current competitive environment (collected for each tree) and the past 100 yr of climate (e.g., monthly temperature and precipitation).

Study site and species—

We collected data in Mt. Rainier National Park, located in the western Cascade Mountains of Washington, United States. Mt. Rainier is a 4392-m-high volcano that has remained relatively undisturbed since its creation as a park in 1899. The park is an excellent study system for investigating climatic controls on range limits because strong climatic gradients exist across a relatively small area, with cooler temperatures and greater amounts of precipitation as elevation increases (Franklin et al., 1988). The climate is temperate maritime, with dry summers and heavy winter precipitation. Soils are podzolic, with surface organic horizons that have accumulated over soil horizons buried from multiple volcanic ash deposits (Franklin et al., 1988).

We sampled three conifer species that are the dominant climax species on Mt. Rainier's south side (Appendix S1), are abundant in the Pacific Northwest, and have ranges that span from northern California to southern Alaska (Franklin et al., 1988; Burns and Honkala, 1990). These included one low-elevation species [*Tsuga heterophylla* (Raf.) Sarg., western hemlock], whose local elevational range extends from below the park boundary (~600 m) up to 1200 m a.s.l., one broad-ranging species (*Abies amabilis* Douglas ex J. Forbes, Pacific silver fir), which occurs from ~700 to ~1600 m a.s.l., and one high elevation species [*Tsuga mertensiana* (Bong.) Carrière, mountain hemlock], which occurs from ~1200 m to treeline (>1600 m a.s.l.) on the south side of Mt. Rainier. Sampling locations (Appendix S1) included the upper elevational range limits of all three species and lower limits for *A. amabilis* and *T. mertensiana* (Franklin et al., 1988). All of our sampling sites occurred in closed canopy forests except the highest site, which was subalpine parkland and consisted of a patchy landscape of tree clumps and meadows.

***Growth data*—**

During summers from 2008 to 2012, we visited seven different elevations on Mt. Rainier's south side. At each elevation, we collected growth data from approximately 20 individuals, per species (when present) and life history stage (saplings and adults), that differed in the competitive environment they experienced. This yielded four to five elevations per species (Appendix S1). Growth data consisted of increment cores for adult trees (previously analyzed by Ettinger et al., 2011) and cross sections for saplings. Individual trees and saplings were located at least 20 m apart from each other, adjacent to one-hectare permanent study stands established in the 1970s by the Permanent Plot Network (Acker et al., 2006). We selected adult trees with diameters at breast height (DBH) greater than 40 cm and collected two cores per individual. We harvested cross sections from saplings that were 1 to 2 m in height.

Increment cores and cross sections were sanded, scanned, and analyzed using the program WinDENDRO (version 2008e, Regent Instruments Inc., Quebec, Canada) to identify annual rings and measure growth. We used standard dendrochronological techniques to identify missing and false rings (i.e., visual crossdating), resulting in annual rings dated to the calendar year (Stokes and Smiley, 1968). For adult trees, we verified the accuracy of visual cross-dating with the Dendrochronology Program Library (dplR) package in R, version 2.15.1 (R Development Core Team, 2009; Bunn, 2010). Quantitative cross-dating was not possible in cross sections, likely due to suppressed growth of saplings (little variation between years in a particular individual, e.g., Colenutt and Luckman, 1995; Parent et al., 2002).

We averaged ring widths from the two collected cores for each individual adult tree. Because of asymmetric growth in sapling cross sections, we measured ring widths along four perpendicular paths radiating out from the center of each cross section; these were then averaged together for average annual ring widths for each year spanning the age of the sapling (range: 14–200 yr, mean = 71.6 yr, median = 64 yr). For climate-growth relationships, we then standardized each tree's or sapling's ring width series by fitting a spline through the time series to remove size-specific trends (Cook and Peters, 1981). We set the spline's rigidity at 100 yr for adults and 30 yr for saplings, and its wavelength cutoff at 50% (e.g., Nakawatase and Peterson, 2006; Littell et al., 2008). More- or less-flexible splines did not qualitatively influence our results. After splining, dimensionless ring-width indices (RWI) were used as a measure of annual tree growth in growth-climate analyses. For growth-competition analyses, the response variable was average individual annual growth (not detrended) over the most recent 10 yr.

Climate data—

We used the same climate data set published in Ettinger et al. (2011). Climate records (1914–2007) came from the Longmire Ranger Station, located within our elevational transect (http://lwf.ncdc.noaa.gov/oa/climate/climatedata.html, online Appendix S2). Longmire climate (842 m a.s.l.) is strongly correlated with climate directly above (Paradise Ranger Station, 1654 m a.s.l.) and below (LaGrande, 293 m a.s.l.) our sampling locations (Ettinger et al., 2011). Over the 94 years included in our study, mean annual temperatures at Longmire ranged from 4.96° to 8.80°C (online Appendix S2) and averaged 6.87°C; there was a weak positive trend in mean annual temperature during this time (slope = 0.01, P = 0.003). Total annual precipitation ranged from 109.8 cm to 302.4 cm (online Appendix S2) and averaged 206.5 cm; there was no trend in total annual precipitation during this time (slope = −0.03, P = 0.986).

On the basis of previous studies and available historic data (Taylor, 1995; Peterson and Peterson, 2001; Nakawatase and Peterson, 2006; Littell et al., 2008; Ettinger et al., 2011), we chose nine climate variables as potential explanatory variables in our analyses: mean annual temperature, mean growing season temperature (May to September), mean dormant season temperature (November to March), total annual precipitation, total growing season precipitation, total dormant season precipitation, maximum size of the snowpack in snow water equivalent, snow duration (the number of days the ground was covered by snow in a given year), and growing degree days (the annual sum of daily mean temperatures for days with mean temperatures above 5°C). All annual variables were calculated for hydrologic years, from October to September of the following year. Tree growth is likely also influenced by potential evapotranspiration (PET) in the Pacific Northwest (e.g., Littell et al., 2008); however, we did not include PET as an explanatory variable because data are available on much shorter time scales than temperature and precipitation. Moreover, PET is highly correlated with the climatic variables we did include (Ettinger et al., 2011).

We combined climate data from Longmire with output from a climate-mapping model called PRISM (Parameter-elevation Regressions on Independent Slopes Model) to estimate a climatic time series at each of our sampling locations. PRISM uses climate station data, digital elevation models, and physiographic-climate relationships to estimate temperature and precipitation on a 30-arcsec (~800 m) grid (Daly et al., 2008). We used climate estimates for the grid cells within which sampling locations were located to create a 1914–2007 time series for annual values of each climate variable at each sampling location (Ettinger et al., 2011).

***Competition data*—**

We compared tree growth in low vs. high competitive environments for both sapling and adult individuals, and to do this, we generated two explanatory variables representing competitive environment: (1) gap status (only for saplings), and (2) the total basal area of neighboring trees. For saplings, we collected roughly equal sample sizes of individuals located either in canopy gaps (low competition) or nongaps (high competition, *N* = 10 per gap status per elevation, in most cases), and additionally quantified the competitive environment around each sapling by measuring the distance to and DBH of all trees greater than 10 cm in diameter, within a 10-m radius of the focal sapling. For adult trees, we also quantified competitive environment by calculating total basal area of neighboring trees, as above, but did not stratify our sampling between canopy gaps and nongaps because the trees we cored were all large enough to be in the forest canopy.

We used average individual annual growth over the most recent 10 yr as the response variable for growth-competition analyses because the competitive environments we measured at the time of data collection (2008–2012) are unlikely to be accurate going far back in time. Large gaps (85 m2 or more) can persist for 25 years (Spies et al., 1990), but the gaps in our study were much smaller and therefore likely to fill in more rapidly (Kane et al., 2011).

***Statistical analyses*—**

Growth–climate relationships—

We used linear mixed-effects models to evaluate the relationship between growth and climate for each species and life stage at each sampling location (for adults, identical to previously published growth–climate relationships in Ettinger et al., 2011). Unlike most standard dendroecological analyses (where analyses are based on average RWIs of all individual trees at a site), mixed-effects models allowed us to accommodate differences among individual tree responses to climate. We designated both individual tree and year as random effects to account for nonindependence of data from the same individual or within years (Crawley, 2007) using a random slopes structure for individual tree and an intercept-only structure for year (Zuur et al., 2009). All climate variables were fixed effects, and we used standardized climate variables in our models (i.e., by subtracting the mean and dividing by the standard deviation) to enable direct comparison of coefficients across elevations. We conducted all statistical tests using the open-source software R, version 2.15.1, and used the lme4 package for fitting mixed-effects models (Crawley, 2007; R Development Core Team, 2009; Bates and Maechler, 2010).

To evaluate which combination of climate variables (if any) best explained annual growth patterns, we fit 32 linear mixed-effects models for each species and life stage at each sampling elevation using maximum likelihood estimates, as in Ettinger et al., 2011). Our models ranged from a null (only an intercept) and all single climate-variable models (models with only mean annual temperature, only growing season precipitation, etc.) to more complicated models with two-way interactions between climate variables (see Ettinger et al., 2011 for a list of models and more details on these methods). The models we fit constitute only a subset of all possible models; we excluded models with highly correlated explanatory variables (r > 0.6, e.g., mean annual temperature and dormant season temperature) and what we viewed as biologically implausible combinations of explanatory variables (e.g., three-way interactions). We used Akaike's information criterion (AIC) to identify the best-fitting climate model for each species at each sampling elevation. We also used the difference in AIC values between the null model and the best-fit model to indicate the extent to which climate explains variation in observed tree growth (AICNull – AICBest). We calculated significance of coefficients using the LanguageR package in R, which estimates P values using Markov chain Monte Carlo (MCMC) sampling (Baayen et al., 2008).

Growth–competition relationships—

We used analysis of variance to evaluate the relationship between recent growth and competition for each species and life stage across all sampling elevations. For the response variable, we averaged recent growth (annual ring width from 1998–2007) for each individual tree or sapling and took the natural log to achieve normality. For saplings, we used preliminary model selection to compare continuous (total basal area of neighboring trees) and categorical ("gap" or "nongap", with gap = low competition and nongap = high competition) explanatory variables. For the continuous explanatory variable, we were unsure of the competitors' zone of influence, so we summed basal area of neighboring trees at one meter increments ranging from one to ten meters. Across all species, we compared model fit for each of these ten continuous competition models with the categorical model, and found that the categorical variable provided better fit, based on AIC (online Appendix S3). We therefore fit a linear model for each species with the following explanatory variables for saplings: categorical competitive environment, sampling elevation (modeled as a categorical variable), and their interaction. For adult trees, we used model selection to compare the 10 continuous competition models (basal area within 1 m, 2 m, 3 m, etc.), across all species. The best-fit model for adult species, based on AIC, was a continuous model using basal area of neighboring trees within 2 m, so we fit linear least squares regression models for each species with continuous competitive environment (basal area of neighboring trees within 2 m), sampling elevation, and their interaction.

We wanted to compare the relative strength of competitive effects on adults vs. saplings, which we could not do by simply comparing coefficients because competitive explanatory variables differed between adults (basal area within 2 m) and juveniles (gap/nongap status). We therefore transformed the continuous competitive effects we calculated for adults to the categorical competitive index we used for sapling models. We did this by first calculating the average difference in summed basal area of neighboring trees between sapling gaps and nongaps at each elevation (using a distance of 2 m, as in the best-fit models for adult trees). We then multiplied this difference in basal area by the elevation-specific competition coefficients from the adult best-fit continuous linear models for each species. These calculations yielded an estimate of high vs. low competitive environment on growth of adult trees analogous to nongap vs. gap environments and allowed us to compare the effects of competition between the two life stages across all species using a paired *t* test.

Results

The strength of growth–climate relationships differed by elevation, tree species, and life history stage (Table 1, Fig. 3). The best climatic predictors of growth, across most elevations, both life stages, and all three species were climate variables related to snowpack (including snow water equivalent and snow duration) and growing season temperature (including mean growing season temperature and growing degree days). Snow water equivalent and snow duration negatively influenced growth across tree ranges, while growing season temperature and growing degree-days positively influenced growth. Growth–climate relationships were stronger in adult trees, compared to saplings, for *A. amabilis* and *T. mertensiana* (Table 1, Fig. 3). *Tsuga heterophylla* showed the opposite trend, with saplings more sensitive to climate than adults at one upper range limit location (Fig. 3A). However, the strength of the growth–climate relationship for this species was relatively weak, with only one life history stage and elevation sensitive to climate, as compared with *A. amabilis* and *T. mertensiana*.

Effects of competition on growth also differed by elevation, tree species, and life history stage (Table 2, Fig. 4). Within species, growth–competition relationships were stronger in saplings than in adult trees, with larger comparable effect sizes. Effect sizes of competition were on average three times greater for saplings than adults (paired t test on sapling species-specific competition coefficients vs. adult corrected coefficients: mean of differences = 0.312 [95% CI: 0.109, 0.516], t = 3.34, df = 12, P = 0.006) and a greater number of elevations showing significantly negative effects of competition on sapling growth than tree growth (Fig. 4). Sapling growth in all three species was negatively affected by competition across their ranges (Table 2). For *T. heterophylla*, across all elevations, growth at the sapling stage was sensitive to competition, while adult growth was not (Table 2, Fig. 4), and competition had the most negative effect at the lowest elevation (mid-elevational range for this species, Fig. 4). For *A. amabilis*, on the other hand, the strongest effect of competition was observed at high elevations at the sapling stage (Fig. 4). Finally, *T. mertensiana* growth was most limited by competition in the middle of its range (1454 m) and at its upper range limit.

Discussion

Our results suggest that controls over elevational range limits are multifaceted for long-lived tree species, which may result in complex range shift dynamics. We observed increased sensitivity to climate at upper range limits for the two species that occur at treeline, as expected if climate controls upper range limits (Fig. 2). However, this increased climate sensitivity was not observed at lower range limits of these two species, nor at the upper range limit of our third species, *T. heterophylla*, which does not reach treeline. Growth was influenced by competitive environment in all species at the sapling stage and in all adult trees except *T. heterophylla,* although not in ways suggesting biotic controls over range limits (Fig. 2). In all, these results suggest that climate change may not have dramatic effects on individual growth and survival throughout large portions of tree ranges (Fig. 1B), unless other life history stages (e.g., seedling establishment, adult mortality) or processes influenced by climate (e.g., disease, disturbance) play a dominant role. Forecasting range shift dynamics under climate change will therefore be difficult without understanding all of these interacting processes.

Biotic vs. abiotic controls on growth of juvenile and adult trees—

We found evidence that abiotic (climate) and biotic (competition) factors influence growth of all focal species throughout their ranges, but we found evidence that climate potentially affects range limits only at treeline. Climate (specifically snow and growing season temperature) affects growth throughout the ranges of our three focal species on Mt. Rainier (Table 1). Large quantities of snow and short growing season lengths appear to limit growth to some extent at all the elevations in our study area, as previous studies in the region have also found (Case and Peterson, 2005; Nakawatase and Peterson, 2006; Littell et al., 2008). However, the strongest effects of snow and short growing season length were found at our highest elevation sites (Table 1, Fig. 3B, C), suggesting these climatic factors may control upper range limits. By contrast, influences of competition on growth were observed throughout the ranges of species, with no consistent pattern across species' ranges (i.e., greater effects at upper or lower range limits, Fig. 2).

We found that climatic and competitive controls on growth varied with life history stage. Juvenile trees are more sensitive to climatic constraints than adult trees (as we expected) for one species (*T. heterophylla*, Fig. 3A), but not for the other two (*A. amabilis* and *T. mertensiana* – Fig. 3B,C). Competitive interactions, however, influenced sapling growth more strongly than for adult trees for all three species (Fig. 4). Other studies in our region have also found that adult trees, especially those in the upper canopy, may be more sensitive to climate than understory saplings due to physiological changes associated with growing in the shade (Teskey et al., 1984a; Teskey et al., 1984b). Indeed, overstory mortality is sometimes high even as juvenile trees continue to thrive in the understory (Segura et al., 1994). Taken together with our results, this variation in sensitivity to climate by life stage highlights the complexity of dynamics that drive species distributions in long-lived organisms and suggests that multiple life stages should be considered in research on realized vs. fundamental niches (Fig. 1).

How would climate and competition interact to influence growth of either juvenile or adult trees? For example, are competitive effects greater in climatically benign years (Levine et al., 2010), or do competitive effects diminish once climatic factors become less limiting (e.g., Dormann et al., 2004)? If the former, then responses to climate change at upper range limits may be more muted than expected as climatic controls on growth could weaken with warming temperatures. By contrast, a decrease in competitive effects on growth as climates warm may speed range expansion at upper range limits. Unfortunately, we were not able to address this issue with our data. The extensive historic climate data available at Mt. Rainier allowed us to exploit annual variation in climate to understand growth–climate relationships, but data on competitive environments were only available for recent years, preventing us from quantifying interactions between climate and competition. Such interactions warrant future study, given their potential to influence responses to climate change (Suttle et al., 2007).

Implications for controls over range limits—

Surprisingly, our data only partially support the classic hypothesis that abiotic factors control species distributions where conditions are harsh (high elevations at Mt. Rainier), while competitive interactions control range limits in more benign conditions (low elevations, e.g., Connell, 1961; Brown et al., 1996; Loehle, 1998; Emery et al., 2001).

Although two species showed the expected growth–climate relationships at upper range limits (greatest climatic sensitivity there, Fig. 1C), none showed evidence of greater sensitivity to competition at lower range limits. Interestingly, both competition and climate influence growth at upper range limits for *A. amabilis* and *T. mertensiana*, suggesting that these potential range limit determinants are not mutually exclusive and may interact to determine species distributions.

In this study, we focus on responses of growth (one measure of performance) to climate and competition across the ranges of three species, highlighting important complexities regarding climatic and competitive controls on performance at different life stages. We believe that growth is a good indicator of overall individual response to climate and competition. Growth is correlated with other aspects of performance, such as reproductive success, which increases with annual growth for adult conifers (Despland and Houle, 1997). Additionally, tree mortality is more likely following years of low growth (Wyckoff and Clark, 2002). Thus, we believe that our results are broadly indicative of the processes that influence population performance of these tree species at range limits.

However, fully understanding population dynamic responses to climate change at range limits will require studying species' entire life histories. For example, rates of range expansions are likely also influenced by seed germination and/or seedling establishment stages, known to be sensitive to both climate (Franklin et al., 1974; Little et al., 1994; Taylor, 1995; El-Kassaby and Edwards, 2001) and competition (Taylor and Shaw, 1983; Gray and Spies, 1997; Lusk and Smith, 1998). By contrast, range contractions could be largely determined by adult tree mortality, which can also be sensitive to climate and competition (Allen and Breshears, 1998; Breshears et al., 2005; Zimmermann et al., 2009; van Mantgem et al., 2009; Luo and Chen, 2011). Understanding how climatic and nonclimatic factors affect these two life stages is critical for forecasting population dynamics at range limits (Fig. 1).

Range shifts in response to climate change—

In keeping with other studies and forecasts, we found that the strongest responses to climate change are likely to occur at ecotones, or where one functional group (trees) replaces another (herbaceous species) (Allen and Breshears, 1998; Kullman, 2002; IPCC, 2007), in this case, at upper range limits (Fig. 1C). We found that climate, specifically snow water equivalent and snow duration, strongly controls growth at treeline, where *A. amabilis* and *T. mertensiana* reach their upper limits (Fig. 3). Given that snowpack is expected to decline by 40% over the next 30 years (compared to 1916–2006 averages) as temperatures rise (Mote and Salathé, 2009), we can expect increased growth at treeline with climate change and likely the spread of populations upward (Fig. 1C). Indeed, historic data suggest that upward shifts have already occurred at high-latitude or high-elevation limits across the world, leading to range expansions (Grabherr et al., 1994; Parmesan et al., 1999; Thomas and Lennon, 1999; Lenoir et al., 2008; Moritz et al., 2008; Harsch et al., 2009; Tingley et al., 2009), including at Mt. Rainier (Rochefort and Peterson, 1996; Stueve et al., 2009).

However, our results also suggest that rapid, dramatic responses to climate change may be the exception, rather than the rule. Changes to the population sizes of our focal species through altered growth of saplings and adults with warming will likely be small across the majority of these species' elevational ranges, because we found weak climate sensitivity in tree performance in closed-canopy forests (Fig. 3). Even if other life history stages not studied here (e.g., adult mortality, seed germination) are sensitive to climate, turnover in forest composition due to climate change is likely to be delayed because population dynamics of these long-lived species are slow (e.g., the 1–2 m tall nonreproductive saplings we harvested were sometimes >100 yr old, and insensitive to climate, Fig. 1B). Recent studies suggesting that some European and North American tree species may still not have fully expanded their ranges following the last glacial maximum (Gavin and Hu, 2006; Svenning and Skov, 2007; Normand et al., 2011) are suggestive of such slow dynamics. These protracted responses would imply that even at high elevations, where climate change effects are expected to be strongest, range shifts will probably lag the velocity of climate change (Loarie et al., 2012). Recent models have also found that interspecific competition (Urban et al., 2012) and other biotic interactions (Fisichelli et al., 2012) can create lags in climate tracking.

There are two caveats to our conclusion that range shifts of these focal species and, thus, forest turnover with climate change, is likely to be slow. First, global change may result in climate conditions outside the current range observed at Mt. Rainier. If focal species exhibit threshold sensitivities to climate, "climatic tipping points" may lead to nonlinear responses and sudden range shifts (Doak and Morris, 2010). Such threshold dynamics would imply that short-term responses to climate change may not match long-term responses. For example, the largest temperature increases are projected during summer months and summer drought is expected to increase (Mote and Salathé, 2009). If severe, such changes could reduce tree growth at low elevations, given that other studies have found Pacific Northwest conifers to be negatively influenced by summer water deficit in populations east of our study area that already experience much drier conditions (e.g., Littell et al., 2008). Although we believe it is unlikely that such drought-related growth reductions would occur in the near future in Mt. Rainier's closed-canopy forests (or in similar forests), since we found minimal evidence of drought stress or water-limitation in our focal species, other "climatic tipping points" may still occur here or elsewhere.

Additional considerations are other indirect effects of climate change (beyond competition) on tree populations. For example, the area burned by fire in the Pacific Northwest is projected to double by the 2040s (relative to 1916–2006 averages), as summer temperatures increase and summer precipitation decreases (Mote and Salathé, 2009). Additionally, pests, such as mountain pine beetle, are expected to increase and reach higher elevations (Kurz et al., 2008; Mote and Salathé, 2009). Neither of these specific indirect climate change effects is currently playing an active role at our sample sites, where the natural fire rotation ranges from 438 to 616 years and Pinus individuals are uncommon (Franklin et al., 1988). However, they exemplify disturbances that could prompt rapid range contractions in the future, and such indirect effects may pose the greatest threat to species persistence under climate change (Swab et al., 2012).

Conclusions—

Overall, our results highlight the complexities of range shift dynamics for long-lived species, such as trees, in the face of global climate change. Unfortunately, these complexities are unlikely to be revealed by current bioclimatic models. Such models would predict, for example, that *Abies amabilis* will shift its range upward by more than 500 m by 2100 with the 2°C warming forecast for the region (Fig. 1A). Our results suggest, however, that range contractions for this species may not keep pace with warming (Fig. 1C), because populations at lower range limits are insensitive to climate (Fig. 3) and strongly influenced by competitive dynamics (Fig. 4), which are slow for these long-lived organisms. Although factors limiting performance at range limits are similar for adults and juveniles of this species, the strength of climatic vs. competitive constraints on populations differed for juveniles vs. adults of this species (Figs. 3, 4), further influencing the dynamics of range shifts in response to climate change. Because *A. amabilis* juveniles are both less sensitive to climate than adults and more sensitive to competition, range expansions at upper limits are actually likely to be slower than predicted by adult responses and may lag changes in climate (Fig. 1B). Thus, bioclimatic models should include both biotic interactions and information from multiple life history stages to increase the reliability of their forecasts.

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TABLES

TABLE 1. Adult tree and sapling climate sensitivity across focal species' ranges. Climate limits growth at some, but not all, range limits in focal species, based on best-fit models, climate coefficients, and the strength of climatic influence on growth (last two columns in table: $\mathrm{AIC}_{\mathrm{Null}} - \mathrm{AIC}_{\mathrm{Best}}$). Climate variables are standardized, so coefficients are directly comparable. Significant effects of climate ($P < 0.05$) are indicated by boldfaced coefficients; italicized coefficients indicate marginally significant effects ($P < 0.1$), based on MCMC sampling. Superscripts on coefficients indicate the exact identity of the season-specific climatic variable in best-fitting models. Growing season precipitation variables were not included in any best-fitting models, and so are left out of the table. N = 20–22 for each species at each sampling location, except for adult *T. mertensiana* at 1197 m a.s.l. ($N = 19$), and sapling *T. heterophylla* at 704 m a.s.l. ($N = 17$). Adult tree growth–climate results (columns 4, 6, 8, and 10) were previously published by Ettinger et al. (2011).

		Effect of climate variables on growth						Strength of climatic influence on growth	
		Temperature (growing season)		Temperature (dormant season)		Precipitation (dormant season)			
Species	Location in range (m a.s.l.)	Sapling	Adult	Sapling	Adult	Sapling	Adult	Sapling	Adult
Tsuga heterophylla	Mid (704)		**-0.046**^{a}			<0.001^{g}		2	4
	Mid (851)		**-0.035**^{a}	*0.046*^{c,h}	**0.030**^{c}	*0.036*^{h,i}		26	12
	Mid (1064)		0.003^{b}					0	9
	Upper (1197)		0.012^{b}			**-0.036**^{f}	-0.006^{e}	6	7
Abies amabilis	Lower (704)					**-0.028**^{i}	-0.026^{e}	2	4
	Mid (1064)					-0.007^{e}		14	0
	Mid (1454)					**-0.019**^{i}	**-0.054**^{e}	3	20
	Mid (1460)		0.006^{b}	**0.025**^{c}			**-0.085**^{e}	7	69
	Upper (1603)	-0.001^{a}	*0.023*^{b}			**-0.042**^{e}	**-0.127**^{e}	30	74
Tsuga mertensiana	Lower (1197)		**0.037**^{b}			-0.021^{e}		16	25
	Mid (1454)		**0.044**^{b}			**-0.042**^{e}	0.024^{e}	14	22
	Mid (1460)		**0.057**^{b}			**-0.036**^{f}		9	21
	Upper (1603)	0.024^{b}	**0.044**^{b}			**-0.040**^{e}	**-0.072**^{e}	50	68

[a] Mean growing season temperature (GST)

[b] Growing degree days (GDD)

[c] Mean dormant season temperature (DST)

[d] Mean annual temperature (MAT)

[e] Snow water equivalent (SWE)

[f] Snow duration (SNDR)

[g] Cumulative precipitation (PPT)

[h] interaction term was not significant

[i] Dormant season precipitation (DPT)

TABLE 2. Effects of competition on adult tree and sapling growth across focal species' ranges. Two-way analyses of variance for adult and sapling focal species suggest that competition limits growth in all sapling species across their ranges, and all adult species except for *Tsuga heterophylla*. Competition is measured categorically (high vs. low competition) for saplings, and continuously (basal area of neighboring trees) for adults, as determined by model selection using AIC. * indicates significance (*P* < 0.05).

		Saplings				Adult trees			
Species	Source of variation	df	SS	MSS	*F*	df	SS	MSS	*F*
Tsuga heterophylla	Competition	**1**	**2.26**	**2.26**	**14.13***	1	0.00	0.00	0.01
	Elevation	3	0.05	0.01	0.09	**3**	**12.93**	**4.31**	**11.69***
	Interaction	**3**	**2.42**	**0.81**	**5.05***	**3**	**5.14**	**1.71**	**4.65***
	Residuals	69	11.00	0.16		69	25.45	0.37	
Abies amabilis	Competition	**1**	**3.90**	**3.90**	**19.52***	1	**1.99**	**1.99**	**5.43***
	Elevation	**4**	**4.07**	**1.02**	**5.09***	**4**	**27.43**	**6.86**	**18.71***
	Interaction	**4**	**3.13**	**0.78**	**3.91***	4	0.75	0.19	0.51
	Residuals	92	18.38	0.20		86	31.53	0.37	
Tsuga mertensiana	Competition	**1**	**2.40**	**2.40**	**7.69***	**1**	**1.81**	**1.89**	**6.52***
	Elevation	3	0.41	0.14	0.44	**3**	**8.10**	**2.69**	**9.71***
	Interaction	3	0.92	0.31	0.98	**3**	**3.69**	**1.23**	**4.43***
	Residuals	72	22.44	0.31		69	19.13	0.277	

Figure Legends

Fig. 1. If climate alone does not determine range limits, anthropogenic warming could lead to complicated range shift dynamics. For example, assume that current observed species' ranges are at equilibrium with their climate niches (top panel). If climate alone controls range limits, species ranges may shift up in latitude and elevation in pace with warming (A). Alternatively, species range shifts may not keep pace with climate, if, for example, populations are insensitive to climate at range limits or competitive effects slow population growth (B). Ranges may expand with warming, if juvenile stages are sensitive to climate, such that they show rapid positive responses (i.e., establishment, growth) to decreased climatic stress at upper limits, while adults are insensitive to changes in climate (C). On the other hand, if adults are more sensitive to climate than juveniles, then range contractions may occur as adult responses (i.e., growth, mortality) at lower limits outpace juvenile establishment at upper limits (D).

Fig. 2. Hypotheses: effects of climate and competition on species' performance should differ across ranges, depending on their relative importance in driving range limits. We expect that, if climate alone is important in driving species distributions and their responses do not vary by life history stage (as climate envelope models assume), then the effects of biotic factors, such as competition, should not vary across the range (A), while effects of climate (i.e., snow, which is important at Mt. Rainier) should be most dramatic at upper and lower limits (B). Alternatively, if competition alone drives range limits (again, with similar responses across life stages), then competition should strongly control growth at range margins (C), while climatic effects on performance should be minimal and not vary consistently across the range (D). Our expectations for focal conifers at Mt. Rainier National Park are based on previous studies and theory; specifically, we hypothesize that competition may drive lower range limits (E), while climate determines upper range limits (F), and that sapling stages are more sensitive than adults to both range limit determinants.

Fig. 3. Effects of climate (snow) vary by life stage and focal species. For *Tsuga heterophylla*, growth at the adult stage is insensitive to snow and other climate variables, while sapling growth is sensitive to snow at its upper range limit (A). For *Abies amabilis* (B) and *Tsuga mertensiana* (C), snow limits adult tree growth more strongly than sapling growth at upper range limits. Bars represent coefficients from linear mixed effects models for climate, with standardized annual snow water equivalent as the explanatory variable; this climate variable is important across many species, elevations, and life stages (Table 1). Snow water equivalent was standardized and growth was measured as detrended ring widths, so coefficients are directly comparable and are filled in when significant ($P < 0.05$).

Fig. 4. Effects of competition differ by life stage and focal species. Across their ranges, focal species were generally negatively affected by competition at both life stages (Table 2). The exception to this was the adult stage of *Tsuga heterophylla* (A), which varied in its response to competitive environment such that one site showed negative effects on growth and another showed positive effects (facilitation). Sapling growth of *T. heterophylla* was consistently negatively affected by competition (B), with the strongest

sensitivity at the lowest elevation (in the middle of its range). *Abies amabilis* growth was negatively affected by competition at both adult (C) and sapling (D) stages, with the greatest sensitivity in saplings at upper range limits. Growth of *T. mertensiana* was also sensitive to competition at both adult (E) and sapling (F) stages, though patterns do not suggest competitive controls on range limits. Bars represent elevation-specific competition coefficients from the best-fit linear least squares regression models for competition (Table 2) and are filled in if competition had a significant effect ($P < 0.05$) at each elevation. Growth is measured as the natural log of average recent growth in millimeters. Coefficients are comparable across elevations within a species, but not across life stages because best-fit models included a categorical measure of competition for saplings and a continuous measure for adults.

Figures

Figure 1.

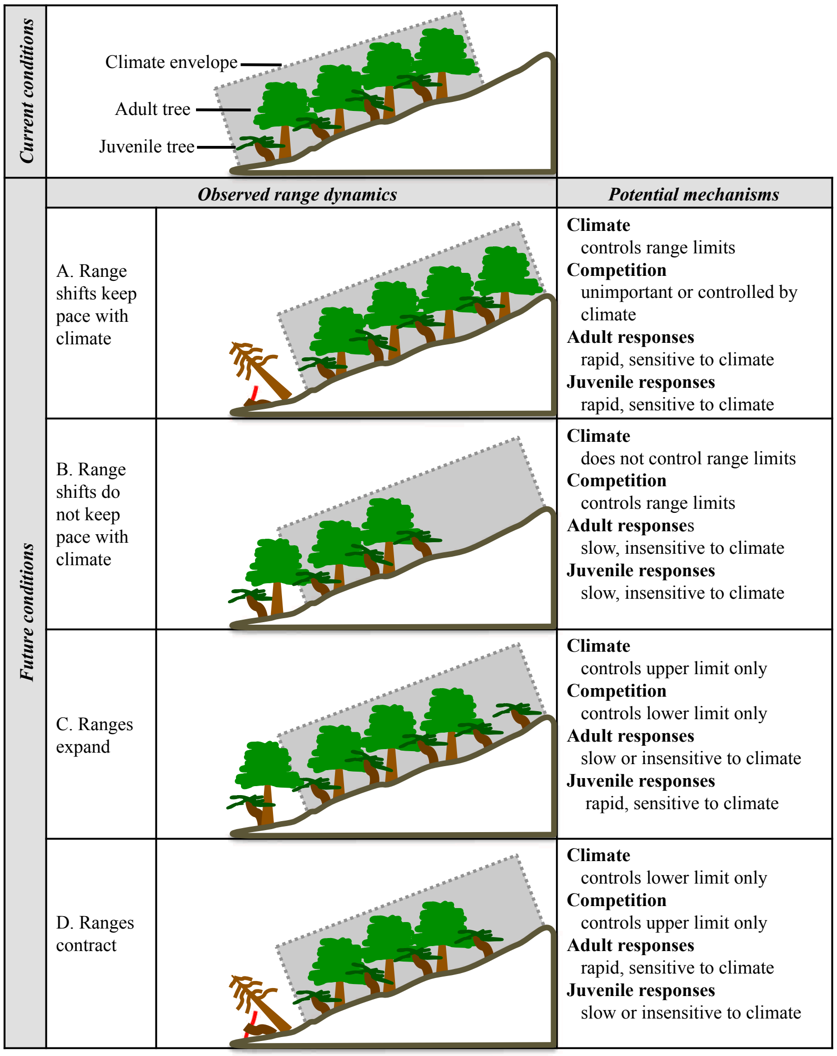
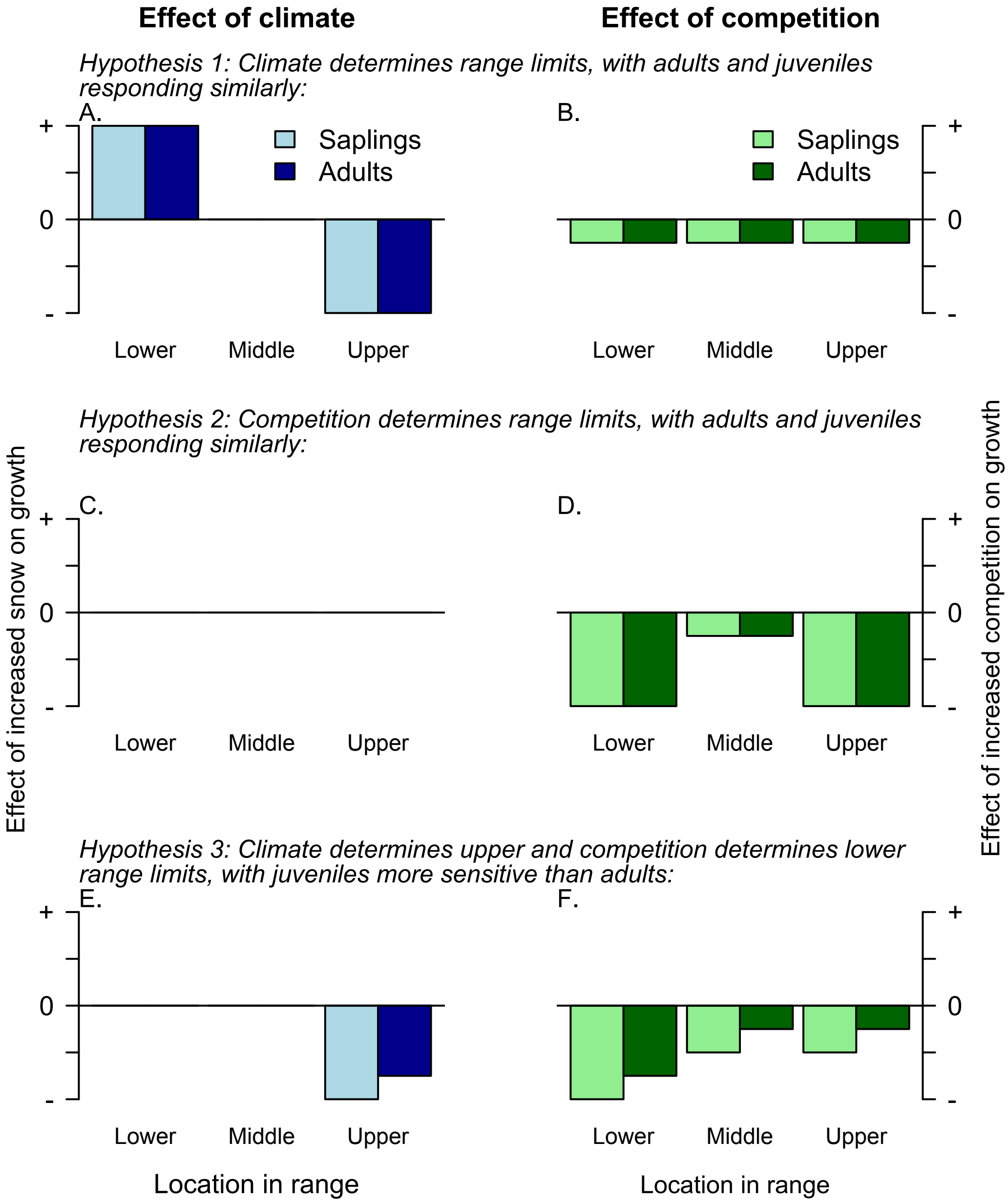


Figure 2.



Effect of climate

Effect of competition

Hypothesis 1: Climate determines range limits, with adults and juveniles responding similarly:

Hypothesis 2: Competition determines range limits, with adults and juveniles responding similarly:

Hypothesis 3: Climate determines upper and competition determines lower range limits, with juveniles more sensitive than adults:

Figure 3.

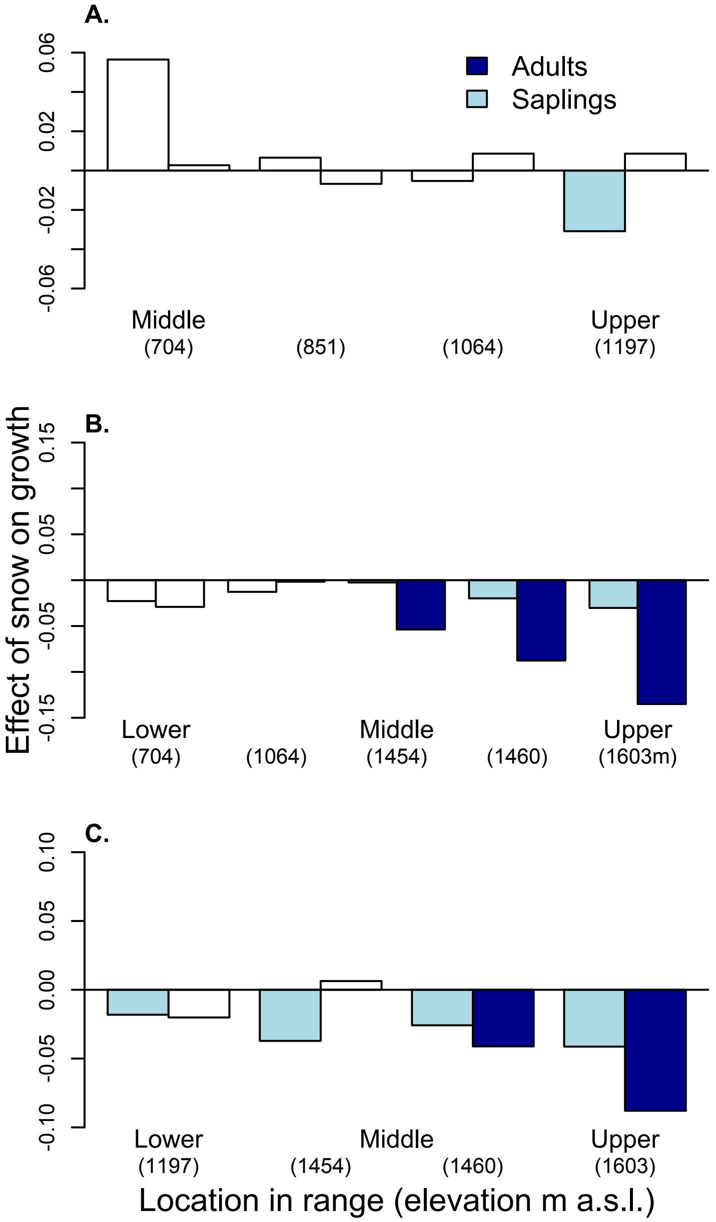
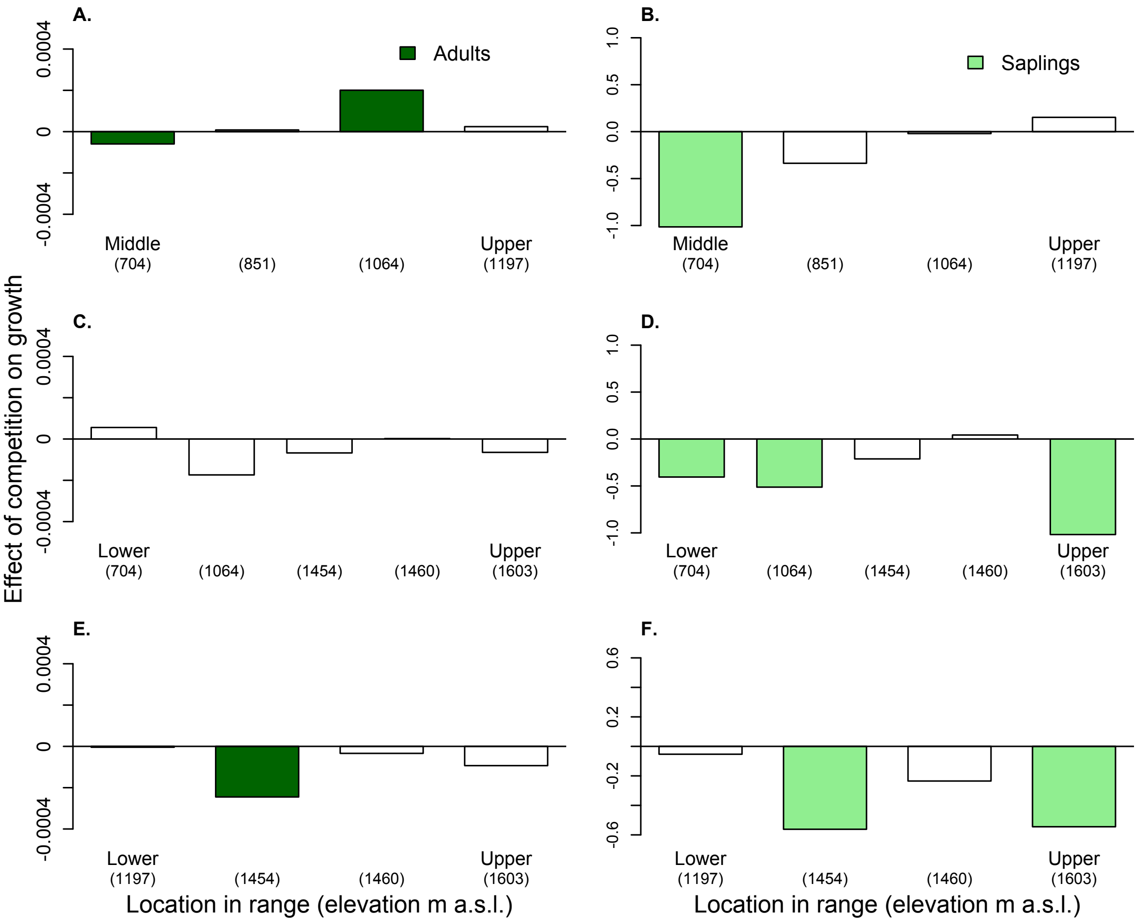

A.
0.06
0.02
-0.02
-0.06
Adults
Saplings
Middle
(704)
(851)
(1064)
Upper
(1197)
B.
Effect of snow on growth
0.15
0.05
-0.05
-0.15
Lower
(704)
(1064)
Middle
(1454)
(1460)
Upper
(1603m)
C.
0.10
0.05
0.00
-0.05
-0.10
Lower
(1197)
(1454)
Middle
(1460)
Upper
(1603)
Location in range (elevation m a.s.l.)

Figure 4.


A.
Adults
0.0004
0
-0.0004
Middle
(704)
(851)
(1064)
Upper
(1197)
B.
Saplings
1.0
0.5
0.0
-0.5
-1.0
Middle
(704)
(851)
(1064)
Upper
(1197)
Effect of competition on growth
C.
0.0004
0
-0.0004
Lower
(704)
(1064)
(1454)
(1460)
Upper
(1603)
D.
1.0
0.5
0.0
-0.5
-1.0
Lower
(704)
(1064)
(1454)
(1460)
Upper
(1603)
E.
0.0004
0
-0.0004
Lower
(1197)
(1454)
(1460)
Upper
(1603)
Location in range (elevation m a.s.l.)
F.
0.6
0.2
-0.2
-0.6
Lower
(1197)
(1454)
(1460)
Upper
(1603)
Location in range (elevation m a.s.l.)

Appendix S1. Supplemental Methods.

Table 1S. Sampling locations. WGS84.

Elevation (m)	Latitude	Longitude	Species Sampled
704	N46.74043	W121.88835	*A. amabilis* *T. heterophylla*
851	N46.74041	W121.84803	*T. heterophylla*
1064	N46.77630	W121.78423	*A. amabilis* *T. heterophylla*
1197	N46.76860	W121.75752	*T. heterophylla* *T. mertensiana*
1454	N46.77626	W121.74793	*T. mertensiana*
1460	N46.76821	W121.74326	*A. amabilis* *T. mertensiana*
1603	N46.77645	W121.73232	*A. amabilis* *T. mertensiana*

Table 2S. Preliminary model selection to identify structure for competition explanatory variable. Categorical and continuous models were fit across all species, to identify the competition index that best explained growth for each life stage. Best-fit models, based on AIC values, are in bold.

	Saplings			**Adults**		
Model	**df**	**AIC**	**ΔAIC**	**df**	**AIC**	**ΔAIC**
Null	2	502	69	2	690	103
Categorical (Low/High Competition)	**15**	**433**	**0**	19	607	20
Continuous (distance=10m)	15	471	38	19	614	27
Continuous (distance=9m)	15	469	36	19	612	25
Continuous (distance=8m)	15	474	41	19	613	26
Continuous (distance=7m)	15	470	37	19	608	21
Continuous (distance=6m)	15	473	40	19	616	29
Continuous (distance=5m)	15	480	47	19	617	30
Continuous (distance=4m)	15	465	32	19	611	24
Continuous (distance=3m)	15	474	41	19	603	16
Continuous (distance=2m)	15	476	43	**19**	**587**	**0**
Continuous (distance=1m)	14[a]	489	56	19	610	23

[a] One coefficient (interaction term at one elevation) not defined because of singularities

CHAPTER 3

Climate, competition, and origin population influence elevational distributions

Introduction

Because scientists often assume that climate drives species' distributions, climate change is expected to cause widespread range shifts (Parmesan 2006, IPCC 2007). Indeed, historical changes in climate have resulted in altered elevational distributions and community compositions of trees, both globally and in the Pacific Northwest (Dunwiddie 1986, Dunwiddie 1987, Prentice et al. 1991, Mclachlan and Brubaker 1995, Davis and Shaw 2001, Gavin et al. In press). Anthropogenic climate change is predicted to occur at unprecedented rates (IPCC 2007), however, and the extent to which climate determines species' ranges remains uncertain (Sexton et al. 2009). While the distributions of many species have moved upward in latitude and elevation with recent rising global temperatures (Parmesan 2006), it is clear that species have responded inconsistently to anthropogenic climate change. Some ranges have shifted, others have expanded or contracted, and many are unchanged (e.g. Moritz et al. 2008, Harsch et al. 2009, Chen et al. 2011). These variable responses to warming suggest that factors other than climate affect species' range limits (Ettinger et al. 2011).

Biotic interactions can also drive species distributions, and may create stable range boundaries, even without environmental gradients (Wethey 2002, Sexton et al. 2009). Many studies document strong effects of competition on species' performance and distributions (e.g. Harmon and Franklin 1989, He and Duncan 2000, Edwards and Hernandez-Carmona 2005, Arif et al. 2007). For example, interspecific competitive interactions appear to restrict the elevational ranges of Neotropical birds (Jankowski et al. 2010) and can affect tree range shift velocity more than does large-scale climate (Meier et al. 2012). However, few empirical studies have explicitly examined competitive interactions across species' ranges (Sexton et al. 2009, but see Ettinger and HilleRisLambers 2013, HilleRisLambers et al. In press).

Range boundaries may also be affected by population-level variation in sensitivity to climate and competition, due to intraspecific genetic differentiation (Chen et al. 2010, Reich and Oleksyn 2008, Leites et al. 2012). Adaptive differentiation has been inferred from common garden experiments conducted around the world, and quantitative trait measurements have enabled estimates of range-wide genetic differentiation for many tree species (Davis and Shaw 2001, Alberto et al. 2013). For example, origin population can lead to intraspecific variation in cold-hardiness, phenology (e.g. budset and bud burst), and growth rates in conifers grown in a common environment (Aitken and Adams 1996, Chuine et al. 2006, Alberto et al. 2013). The extent to which seeds are "preadapted" to changes in climate, because of their origin population, may affect current and historic range boundaries, as well as future climate change-induced shifts in species' ranges (Davis and Shaw 2001).

To better understand how climate, competition, and origin population interact to determine species distributions, we examined how competition (both canopy and understory) and origin population affect tree survival and growth across an elevational and climatic gradient on Mt. Rainier, Washington, USA. Specifically, we conducted a seedling transplant experiment, moving seedlings within and beyond their elevational ranges in areas differing in the extent of aboveground competition, to ask 1) does survival and growth peak in the middle of species' ranges; 2) are competitive effects on seedling survival and growth greatest at and beyond range limits; and 3) does origin population constrain performance? We focus on tree seedlings, as establishment plays a critical role in determining range boundaries, particularly at the leading edge, as well as the pace at which range shifts will occur (Smith et al. 2003).

We expected survival and growth to be highest in the middle of species' ranges, following classic fundamental niche theory and common assumptions by natural resource managers (Fig. 1, Gauch and Whittaker 1972, Rydin 1997, Schwartz 2012). Given the heavy winter snowpack at Mt. Rainier's high elevations, we hypothesized that climate (specifically snow duration and growing degree days) determines upper range limits of focal species, while competition drives lower range limits (Ettinger et al. 2011, Ettinger and HilleRisLambers 2013.). Therefore, we expected that negative effects of competition on performance (i.e. growth and survival) would be strongest at low elevations (Fig. 1B). 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 competition treatment at and above upper limits. Furthermore, we hypothesized that origin population plays an important role in tree responses to climate such that tree performance is highest when individuals are grown in their "home" elevation and its associated current climate (Fig. 1C).

Methods

Study site

We conducted the transplant experiment on the southwest side of Mt. Rainier National Park (Fig. 2A), located in the western Cascade Mountains of Washington state. Mt. Rainier is a 4,392-meter high volcano that has remained relatively undisturbed by anthropogenic activities since its creation as a park in 1899. Strong climatic gradients exist on Mt. Rainier, with cooler temperatures and greater amounts of precipitation as elevation increases (Franklin et al. 1988). The climate is temperate maritime, with dry summers and heavy winter precipitation, characterized by large quantities and long durations of snow, particularly at high elevations (Ford et al. In press).

Focal species

We studied three conifer species that are dominant, climax trees on Mt. Rainier's south side, are abundant in the Pacific Northwest, and have ranges that extend from Northern California to Southern Alaska (Franklin et al. 1988, Burns and Honkala 1990). These included one high elevation species (*Tsuga mertensiana* (Bong.) Carrière [mountain hemlock]), which occurs from ~1200 m to treeline (>1600 m) on the south side of Mt. Rainier, one broad-ranging species (*Abies amabilis* Douglas ex J. Forbes [Pacific silver fir]), which occurs from ~700m to ~1600m, and one low elevation species (*Tsuga heterophylla* (Raf.) Sarg. [western hemlock]), whose local elevational range spans from below the Park boundary (~600 m) up to ~1200 m. Transplant sites were located above, at, and in the middle of the Park's elevational range limits of all three species, and also at and below lower limits for *A. amabilis* and *T. mertensiana* (Franklin et al. 1988) (Fig. 2B). All transplant sites occurred in closed canopy forests, except the two highest elevations, which were located in subalpine parkland, consisting of a patchy landscape of tree clumps and meadows.

Experimental design

We established the experiment at seven different elevations on the south side of Mt. Rainier (Fig. 2A&B), and transplanted seedlings of each focal species at five of these elevations: in the middle of a given species' range, at its upper and lower current 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 to only three elevations). Each of the seven elevations contained plots for two of the three focal tree species, with five blocked replicate plots of each treatment at each elevation.

We evaluated differences in canopy competition versus shrub layer competition by establishing transplant plots in forest canopy gaps and non-gaps at each elevation (Fig. 2C). Canopy gaps were identified first, adjacent to one-hectare permanent study stands established in the 1970s by the Permanent Plot Network (Acker et al. 2006) and located at least 20 m apart from one another. Each non-gap site was established 10 m away (in a random direction) from its paired gap. Within each canopy gap or nongap site, we established paired 0.25 m^2 plots and removed all aboveground competition in a half-meter radius around one of the plots in each pair. Each plot was then planted with 15 or 16 seedlings (15 for *T. mertensiana*, 16 for *A. amabilis* and *T. heterophylla*) of one of the focal species. Aboveground vegetation was removed every month during the 2011 and 2012 growing seasons.

To investigate effects of origin population on survival and growth, we transplanted conifers grown from seed collected throughout their elevational ranges on Mt. Rainier. In the fall of 2009, we collected seeds from focal species' populations located in the middle of species' ranges, and at upper and lower range limits (except for *T. heterophylla*). We collected new cones from the forest floor underneath approximately 20 different individuals per species at each elevation. Cones were then dried in a 40°C oven so that they opened to release seeds. We cleaned seeds by soaking them in a 6% bleach solution for 10 minutes, and then flushed them with running water for 12 hours. Seeds were stratified in a 0°C cold room for 8 weeks, and sowed in the greenhouse at University of Washington in Seattle. After true leaves emerged, seedlings were transplanted to 15 cm "Cone-tainers", placed outside, and watered daily until September 2010. At this point their initial height was measured (from ground surface to apical bud) and they were transplanted into plots on Mt. Rainier, where they were watered on the day of transplanting only. In 2011 and 2012, we censused seedling survival twice annually, in the spring and fall. We measured seedling height (from ground surface to apical bud) annually, in the fall.

Measurements of microclimate, light, canopy cover, and soil characteristics

We wanted to quantify variation in climate among and between competition treatments along the elevational transect, both to confirm the expected climatic gradients with elevation and to understand whether canopy and understory vegetation affect microclimate (Ford et al. In press). We used HOBO® Pendants to collect measurements of soil surface temperature every two hours throughout the growing season (measurements were collected every 3 hours during the dormant season). These measurements were used to calculate snow duration and growing degree days (GDD, which we defined as the number of days with an average temperature above 5°C) for each replicate 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. Visible light was measured every two hours during the growing season, using HOBO® Pendants (data were collected every 3 hours during the dormant season). We also measured photosynthetic active radiation (PPFD-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 for each gap or non-gap using a densiometer. We collected soil samples from each gap and non-gap in September 2011. Five soil cores (15 cm deep) were collected from each gap and non-gap, and depths of O and A horizons were measured on each core. Soil cores were pooled by site, 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

Survival- For each species, we fit generalized linear mixed-effect models with a binomial response variable for survival and a random effect of block (i.e. each gap/non-gap pair), using an intercept-only structure (1|Block). We conducted model selection to identify the best-fit model by beginning with a complex mixed-effect model that included all explanatory variables and interactions (i.e. Planted Elevation * Understory Presence* Canopy Presence *Origin Elevation). Models were subsequently simplified, and terms were individually deleted if a simpler model did not have significantly less explanatory power than the more complex one, using Likelihood Ratio Tests (LRTs). The ratios between the likelihoods of the more complex and simpler model were tested using χ^2 reference distributions with degrees of freedom equal to the difference in number of parameters between the two models. At the end of the process, the final model also showed lower Akaike Information Criterion (AIC) values with respect to all previous and more complicated tested model permutations.

Growth- For each species, we fit linear mixed-effect models with relative growth rate [(Final height-Initial height)/Initial height] as the response variable and with a random effect of block, using an intercept-only structure. Model selection was conducted in the same manner described above for survival analyses.

Microclimate, light, canopy cover & soil characteristics- We tested how elevation, canopy presence, and understory presence affected microclimate and light by fitting generalized linear mixed-effect models with Poisson distributions for snow duration, GDD, and light each as response variables and with a random effect of block using an intercept-only structure. As for survival and growth data, we conducted model selection to identify the best-fit model by beginning with a complex mixed-effect model that included all explanatory variables and interactions (i.e. Elevation * Understory Presence * Canopy Presence) and subsequently simplifying models by individually deleting terms based on significance, using LRTs. Canopy cover and soil characteristics were collected at the block level, so we used linear models with only elevation and canopy presence as explanatory variables, and followed the above model selection procedure.

All statistical analyses were conducted in R, Version 2.15.1 using the lme4 package for mixed-effect modeling.

Results

Effects of elevation on survival and growth

Survival and growth varied across species' ranges, but was not highest in the middle of the range. For all three species, survival was highest at upper and/or lower range limits (Fig. 3A-C). Growth, on the other hand, declined with elevation, so it was highest below the lower range limits for *A. amabilis* and *T. mertensiana* (Fig. 3D&E), and highest in the middle of the range for *T. heterophylla* (Fig. 3F). Over the course of the experiment, we measured negative growth in some seedlings. Height did not actually decline; these measurements were due to transplant plugs sinking and litter and duff accumulating on top of the root crown.

Effects of competition on survival and growth

Competition treatment affected survival and growth for all three species. Throughout most of their ranges, both canopy and understory presence negatively affected survival, although canopy presence had a stronger negative effect (i.e. larger coefficients Fig. 4, Tables 1-3). Above upper range limits, however, canopy presence positively affected survival. Growth was negatively affected by canopy presence, but not by understory presence (i.e. best-fit models included only canopy treatment, Tables 4-6), and these negative effects were strongest at low elevations (Fig. 4).

Effects of origin population on survival and growth

Effects of origin elevation on survival and growth varied by species. For survival and growth of *T. mertensiana*, best-fit models included interactions between planted elevation and origin elevation, indicating that effects of origin vary across the range (Tables 1 & 4). Seedlings from upper limit origins for this species tended to have higher survival than those from lower limit origins, when grown at upper limits and beyond upper limits, but seedlings from lower limit origins did better at lower limits (Fig. 5). Growth in *T. mertensiana* was variable, but was generally lowest in individuals from upper limit origin stands, across all elevations (Fig. 5, Table 4). For *Abies amabilis*, however, the effect of origin population was consistent across its elevational range (i.e. best-fit models did not include an interaction between planted elevation and origin, Tables 2 & 5). Throughout the range of *A. amabilis*, survival was highest for individuals from one of the mid-range origin populations and growth was highest in individuals from the upper limit origin population (Fig. 5). While origin elevation did not affect survival of *T. heterophylla* (i.e. origin was not included in the best-fit model, Table 3), growth was affected: individuals from the mid-range stand grew more across all three elevations, with the largest difference above upper range limits (Fig. 5, Table 6).

Microclimate, light, canopy cover, and soils

Snow duration increased with elevation and was negatively affected by canopy presence across the elevational gradient (Fig. 6), but was not affected by understory vegetation (i.e. understory was not included in best-fit models, Table 7). Growing degree days decreased with elevation, and canopy and understory presence had weak positive effects at and above 1197 m in elevation, but not at lower elevations (Fig 6, Table 8). Light levels did not vary consistently with elevation, and were negatively affected by both canopy and understory vegetation (Fig. 6, Table 9). 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. Total soil carbon, hydrogen, and nitrogen levels varied with elevation, but were not affected by canopy presence (Table 10).

Discussion

Does survival and growth peak in the middle of species ranges?

Our results do not support niche theory, which generally assumes that survival or growth should be greatest in the middle of ranges. Instead, all of the focal species experienced low overall survival and growth (across all competition treatments and origins) in the middle of their ranges; there was higher survival at one or both range limits (Fig. 3). Additionally, highest height growth was at the lowest elevations for all species. Niche theory generally assumes continuous, evenly distributed response curves, with optimal performance and abundance in the middle of species' ranges (Gauch and Whittaker 1972, Rydin 1997, Heikkinen and Makipaa 2010). This assumption has led to a number of ecological and evolutionary hypotheses with basic and applied importance, such as that speciation is more likely to occur at range edges, that populations in the center of species ranges are sources while edge populations are sinks, and that central populations are more critical to protect and monitor than edge populations (Sagarin et al. 2006). These findings, combined with the many other studies that have also failed to observe peak performance at range centers, suggest that these hypotheses 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) .

Our results also suggest that current climate is not the primary determinant of lower range limits for conifers on the south side of Mt. Rainier. For example, we did not observe strong evidence that climate determines lower range margins (i.e. that survival and growth are greatly reduced, regardless of competitive environment, at and below current lower range limits, Fig. 3). Other studies in this region have also found that tree performance is not strongly controlled by climate at low elevations (Holman and Peterson 2006, Ettinger et al. 2011).

At upper range limits, evidence for climatic controls on tree performance is mixed, differing for survival versus growth. Surprisingly, we observed higher survival at and above upper limits compared with range centers for *T. mertensiana* and *A. amabilis* (Fig. 3). We had expected that overall survival would be lower above species' natural ranges, if climate determines species' range limits. However, this was generally not the case, except for *T. heterophylla* when planted above its upper elevational range limit (Fig. 3), and may suggest that nonclimatic factors also affect survival and/or that current adult tree ranges do not overlap perfectly with their climate niches, perhaps due to warming since establishment. We observed that tree growth, on the other hand, steadily declined with rising elevation, as expected if the increasing climatic stress along this gradient limits growth. The heavier snowpack, shorter growing season lengths, and lower temperatures found at higher elevations are thought to limit tree growth in the mountains of the Pacific Northwest (Peterson and Peterson 2001, Nakawatase and Peterson 2006, Ettinger et al. 2011), and elsewhere around the world (Körner 1998, Körner and Paulsen 2004).

Are competitive effects on seedling growth and survival greatest at and below range limits?

We found that competition (presence of understory and canopy vegetation) affected survival and growth throughout the ranges of all focal species, but effects did appear to be strongest at and below lower range limits. For example, canopy competition had the largest negative effect on survival of *T. mertensiana* below lower limits and the weakest at and above upper limits (Fig. 4). In addition, for *A. amabilis* growth, canopy competition had the most negative effect below lower range limits, and effect sizes gradually decreased with elevation (Fig. 4).

For what resource(s) are tree seedlings competing? While our methods did not allow us to directly answer this question, we believe that light competition is likely, particularly in the low-elevation, closed canopy sites in our study. We observed reduced visible light and photosynthetic active radiation levels with canopy presence (Tables 9&10), and light is known to be an important limiting resource in Pacific Northwest forests, where natural conifer seedling establishment and growth are often greater in canopy gaps (Gray and Spies 1997, Littell et al. 2009). Water and nutrient competition can also affect plant performance (Holmgren et al. 1997, Coomes and Grubb 2000), but soil moisture, organic content, and nutrients did not differ between canopy gaps and non-gaps in most cases (Table 10).

For the two species that reach treeline (*A. amabilis* and *T. mertensiana*), survival above the upper limits was higher with canopy presence, suggesting facilitative rather than competitive interactions (Fig. 4). Facilitation is well documented in high elevation mountain environments (e.g. Callaway 1998, Choler et al. 2001) , and may play a dominant role in establishing treeline (Smith et al. 2003). It is likely that canopy trees ameliorate some of the climatic stress found in our subalpine study sites; facilitation from canopy, rather than understory, vegetation may be important because of how it alters microclimate at high elevations (Fig. 6, Tables 7 & 8). For example, at the highest elevation in this study (1650m, treeline), canopy absence extended snow duration by 15 days and reduced growing degree days by 21 days, on average. This means that areas without canopy vegetation (gaps) have a 6% shorter snow-free season and 38% fewer growing degree days than areas with canopy present at this elevation (Table 10).

Does origin population constrain performance?

While origin population influenced survival and growth, we did not find strong evidence of local adaptation across all focal species nor that origin is a primary constraint on performance at range limits (Fig. 5). *Tsuga mertensiana* was the only species that showed a survival trend suggestive of local adaptation at range limits (Fig. 1C). Seedlings from upper limit origins generally had higher survival than those from lower limit origins when grown at upper limits and beyond upper limits, and seedlings from lower limit origins had higher survival at lower limits (Fig. 5). Growth patterns in *Tsuga heterophylla* were suggestive of reduced fitness in individuals from upper range limits compared with mid-range (i.e. seedlings from upper limits had lower growth at all elevations). On the other hand, *Abies amabilis* individuals from upper limits had higher growth than those from other origins, even at low elevations (Fig. 5). Forestry practices often assume that seed zones should be selected based on their home climate, but these results suggest that, at least on this relatively small scale, origin climate is not a good predictor of growth or survival in a different climate. Thus, a variety of seed zones should be tested, since origin effects on survival and growth appear to vary by species and site.

Other studies have found stronger effects of origin (or “provenance”) on conifer growth when grown in common gardens (e.g. Campbell 1991, Carter 1996, Leites et al. 2012) , and these results may differ because we focused on different species, younger tree seedlings, and/or populations that are fairly short distances away from one another. This transect spanned approximately 27 kilometers (Fig. 2), but 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), so there may be geneflow between individuals across the range, such that local adaption is weak at range limits along this elevational gradient. It is also possible that, given the long-lived nature of these focal species in Mt. Rainier’s forests (canopy trees at our study sites are 300-800 years old (Franklin et al. 1988)), individuals from which seed were collected may have established at a time when climate differed from current climate. Regardless, competition, especially from canopy vegetation, appears to play a more important role in range limits for these species, given its greater effects on survival and growth compared with origin (i.e. larger coefficients in best-fit models, Tables 1-6).

Conclusion & Implications

We found strong effects of competition, with weaker effects of origin population, on survival and growth across the elevational ranges of focal conifers. Performance was particularly limited by competition at lower range limits, where climate appears to be less stressful. Because competition, not climate, limits performance at lower range margins, climate change is unlikely to cause range contractions in these locations, at least in the short term. Range expansions upward are likely, though, because climate influences performance more strongly at high elevation upper limits (Ettinger et al. 2011). Our results suggest that climate and competition are not mutually exclusive range limit determinants, however, as competitive environment also influences performance at upper limits. At treeline, climate change-induced range expansions will probably occur first where existing adult tree patches will spread outward and upward, since facilitation by canopy trees plays an important role in performance. The strong effects of competition found in our study suggest that scientists and natural resource managers should consider important biotic interactions such as competition when forecasting and planning for climate change-induced range shifts.

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Tables

Table 1. Best-fit model summary for *Tsuga mertensiana* survival. Fixed effect coefficients and standard error, and standard deviation for the random effect (in units comparable to the response variable) are shown from the best-fit generalized linear model, with a binomial response variable. Coefficients include planted location, competition treatment, origin, and interactions.

Fixed Effects	Estimate	Std.Error
Below lower limit	-0.63	0.41
Lower limit	0.23	0.36
Mid-range	-0.41	0.39
Upper limit	-0.58	0.37
Above upper limit	-1.80	0.40
Understory Competition	-0.72	0.35
Canopy Competition	-3.23	0.63
Mid-range Origin	0.53	0.42
Upper limit Origin	0.36	0.43
Understory*Canopy	-0.53	0.27
Below lower limit*Mid-range Origin	-0.84	0.52
Lower limit*Mid-range Origin	-0.12	0.56
Upper limit*Mid-range Origin	-0.21	0.53
Above upper limit*Mid-range Origin	0.23	0.54
Below lower limit*Upper limit Origin	-0.82	0.52
Lower limit*Upper limit Origin	0.17	0.56
Upper limit*Upper limit Origin	0.86	0.53
Above upper limit*Upper limit Origin	0.52	0.54
Below lower limit*Canopy Competition	3.11	0.68
Lower limit*Canopy Competition	2.63	0.70
Upper limit*Canopy Competition	2.58	0.68
Above upper limit*Canopy Competition	4.65	0.69
Below lower limit*Understory Competition	0.19	0.44
Lower limit*Understory Competition	-1.09	0.49
Upper limit*Understory Competition	0.80	0.44
Above upper limit*Understory Competition	0.39	0.46

Random Effects	Std. Dev.
Block	0.50

Table 2. Best-fit model summary for *Abies amabilis* survival. Fixed effect coefficients and standard error, and standard deviation for the random effect (in units comparable to the response variable) are shown from the best-fit generalized linear model, with a binomial response variable. Coefficients include planted location, competition treatment, origin, and interactions.

Fixed Effects	Estimate	Std.Error
Below lower limit	0.01	0.42
Lower limit	0.62	0.41
Mid-range	-0.17	0.41
Upper limit	0.24	0.40
Above upper limit	-1.81	0.44
Understory Competition	-0.77	0.29
Canopy Competition	-1.66	0.30
Mid-range origin (1064 m)	-0.37	0.18
Mid-range origin (1197 m)	0.33	0.16
Upper limit origin	0.15	0.17
Lower limit*Understory Competition	-0.03	0.39
Mid-range*Understory Competition	0.09	0.42
Upper limit*Understory Competition	0.24	0.38
Above upper limit*Understory Competition	1.27	0.40
Lower limit*Canopy Competition	0.37	0.40
Mid-range*Canopy Competition	-0.42	0.46
Upper limit*Canopy Competition	0.72	0.39
Above upper limit*Canopy Competition	3.88	0.42

Random Effects	Std. Dev.
Block	0.74

Table 3. Best-fit model summary for *Tsuga heterophylla* survival. Fixed effect coefficients, standard error, and standard deviation for the random effect (in units comparable to the response variable) are shown from the best-fit generalized linear model, with a binomial response variable. Coefficients include planted location, competition treatment, and interactions.

Fixed Effects	Estimate	Std.Error
Mid-range	-0.84	0.58
Upper limit	-0.22	0.60
Above upper limit	-1.87	0.62
Understory Competition	-2.13	0.54
Canopy Competition	-1.60	0.46
Upper limit*Understory Competition	0.23	0.69
Above upper limit*Understory Competition	-0.69	1.20
Upper limit*Canopy Competition	0.20	0.62
Above upper limit*Canopy Competition	1.00	0.67
Understory Competition*Canopy Competition	-13.12	681.23
Upper limit*Understory Competition*Canopy Competition	15.91	681.23
Above upper limit*Understory Competition*Canopy Competition	13.71	681.24

Random Effects	Std. Dev.
Block	1.17

Table 4. Best-fit model summary for *Tsuga mertensiana* growth. Fixed effect coefficients and standard error, and standard deviation for the random effect (in units comparable to the response variable) are shown from the best-fit linear model. Coefficients include planted location, competition treatment, origin, and interactions.

Fixed effects	Estimate	Std. Error
Below lower limit	0.74	0.13
Lower limit	0.77	0.10
Mid-range	0.65	0.13
Upper limit	0.49	0.11
Above upper limit	0.30	0.14
Canopy Competition	-0.61	0.29
Mid-range Origin	0.31	0.16
Upper limit Origin	-0.21	0.16
Below lower limit*Canopy Competition	-0.10	0.29
Lower limit*Canopy Competition	-0.03	0.30
Upper limit*Canopy Competition	0.17	0.30
Above upper limit*Canopy Competition	0.44	0.30
Below lower limit*Mid-range Origin	-0.39	0.19
Lower limit*Mid-range Origin	-0.59	0.21
Upper limit*Mid-range Origin	-0.74	0.20
Above upper limit*Mid-range Origin	-0.50	0.21
Below lower limit*Upper limit Origin	0.11	0.19
Lower limit*Upper limit Origin	-0.13	0.21
Upper limit*Upper limit Origin	-0.21	0.20
Above upper limit*Upper limit Origin	-0.05	0.21
Canopy Competition*Upper limit Origin	0.24	0.12
Canopy Competition*Upper limit Origin	0.35	0.11

Random effects:	Std. Dev
Block	0.12

Table 5. Best-fit model summary for *Abies amabilis* growth. Fixed effect coefficients and standard error, and standard deviation for the random effect (in units comparable to the response variable) are shown from the best-fit linear model. Coefficients include planted location, competition treatment, origin, and interactions.

Fixed effects:	Estimate	Std. Error
Below lower limit	0.43	0.05
Lower limit	0.34	0.05
Mid-range	0.31	0.06
Upper limit	-0.19	0.05
Above upper limit	-0.15	0.08
Canopy Competition	-0.52	0.09
Mid-range origin (1064 m)	0.07	0.05
Mid-range origin (1197 m)	0.05	0.05
Upper limit origin	0.22	0.05
Lower limit*Canopy Competition	0.25	0.12
Mid-range*Canopy Competition	0.22	0.15
Upper limit*Canopy Competition	0.36	0.12
Above upper limit*Canopy Competition	0.52	0.12
Random effects:	Std. Dev	
Block	0.00	

Table 6. Best-fit model summary for *Tsuga heterophylla* growth. Fixed effect coefficients, standard error, and t-values and standard deviation for the random effect (in units comparable to the response variable) are shown from the best-fit linear model. Coefficients include planted location, competition treatment, origin, and interactions.

Fixed effects:	Estimate	Std. Error
Mid-range	0.94	0.09
Upper limit	0.75	0.08
Above upper limit	0.36	0.13
Canopy Competition	-0.76	0.20
Upper limit origin	-0.35	0.09
Upper limit*Canopy Competition	0.22	0.20
Above upper limit*Canopy Competition	0.61	0.26
Canopy Competition*Upper limit Origin	0.35	0.14
Random effects:	St. Dev	
Block	0.00	

Table 7. Best-fit model summary for snow duration. Fixed effect coefficients and standard error are shown from the best-fit generalized linear model mixed effects model, fit with a Poisson-distributed response variable. Coefficients included elevation and canopy presence only.

Fixed effects:	Estimate	Std. Error
Elevation_m668	3.88	0.03
Elevation_m704	4.19	0.03
Elevation_m1064	5.26	0.02
Elevation_m1197	5.39	0.02
Elevation_m1460	5.52	0.02
Elevation_m1603	5.56	0.02
Elevation_m1650	5.58	0.02
CanopyPresent	-0.06	0.01
Random effects:	St. Dev	
Block	0	

Table 8. Best-fit model summary for growing degree days. Fixed effect coefficients and standard error are shown from the best-fit generalized linear mixed effects model, fit with a Poisson-distributed response variable. Coefficients included elevation, competition treatments, and interactions between competition treatments and elevation.

Fixed effects:	Estimate	Std. Error
Elevation_m668	5.29	0.06
Elevation_m704	5.24	0.06
Elevation_m1064	4.90	0.06
Elevation_m1197	4.67	0.06
Elevation_m1460	4.29	0.07
Elevation_m1603	3.92	0.08
Elevation_m1650	3.69	0.11
CanopyPresent	-0.01	0.04
UnderstoryPresent	-0.01	0.04
Elevation_m704*CanopyPresent	0.00	0.06
Elevation_m1064*CanopyPresent	0.01	0.07
Elevation_m1197*CanopyPresent	0.09	0.07
Elevation_m1460*CanopyPresent	0.58	0.08
Elevation_m1603*CanopyPresent	0.18	0.10
Elevation_m1650*CanopyPresent	0.47	0.12
Elevation_m704*UnderstoryPresent	0.01	0.06
Elevation_m1064*UnderstoryPresent	0.00	0.07
Elevation_m1197*UnderstoryPresent	0.00	0.08
Elevation_m1460*UnderstoryPresent	-0.01	0.09
Elevation_m1603*UnderstoryPresent	0.03	0.10
Elevation_m1650*UnderstoryPresent	0.11	0.13
Random effects:	St. Dev	
Block	0.01	

Table 9. Best-fit model summary for visible light (in lux). Fixed effect coefficients and standard error and standard deviation for the random effect (in units comparable to the response variable) are shown from the best-fit linear mixed effects model. Coefficients included elevation, competition treatment, and an interaction between canopy and elevation.

Fixed effects:	Estimate	Std. Error
Elevation_m668	1465.90	137.19
Elevation_m704	1784.20	137.19
Elevation_m1064	1246.89	145.66
Elevation_m1197	1060.04	137.19
Elevation_m1460	1249.62	137.19
Elevation_m1603	849.36	137.19
Elevation_m1650	1828.21	155.87
CanopyPresent	-667.61	201.63
UnderstoryPresent	-624.04	99.27
Elevation_m704*CanopyPresent	-464.62	263.95
Elevation_m1064*CanopyPresent	-175.62	267.43
Elevation_m1197*CanopyPresent	187.81	263.95
Elevation_m1460*CanopyPresent	42.50	263.95
Elevation_m1603*CanopyPresent	103.71	263.95
Elevation_m1650*CanopyPresent	-549.86	275.00
CanopyPresent*UnderstoryPresent	636.02	140.39
Random effects:	St. Dev	
Block	0.002	

Table 10. Climate, light, vegetation, and soil characteristics by elevation and canopy status. Mean values, across 5 replicates at each elevation, are listed. Bolded text indicates significant differences between gaps and non-gaps. (Abbreviations: Elev= Elevation, PAR=Photosynthetic Active Radiation, C=total soil carbon, H= total soil hydrogen, and N= total soil nitrogen)

Elev (m)	Canopy Status	Snow duration (# days)	Growing degree days (#)	Canopy Cover (%)	Visible light (Lux)	PAR (μmol s^{-1} m^{-2})	Soil Moisture (%)	Organic content (%)	C (%)	H (%)	N (%)
668	Gap	52	198	**82.15**	**1154**	**34**	1.43	5.1	2.9	0.14	0.14
	Non-gap	41	198	**94.9**	**803**	**26**	1.38	5.7	3.3	0.12	0.12
704	Gap	67	189	**82.3**	**1472**	**34**	3.21	15.5	8.9	0.24	0.24
	Non-gap	62	187	**93.1**	**658**	**13**	2.07	12.8	7.3	0.22	0.22
1064	Gap	192	133	**77.6**	**900**	**116**	1.63	19.1	11.0	0.20	0.20
	Non-gap	184	132	**94.0**	**410**	**26**	1.63	14.6	8.4	0.14	0.14
1197	Gap	224	**107**	**77.9**	**748**	**95**	4.50	22.4	12.9	0.26	0.26
	Non-gap	203	**116**	**93.5**	**586**	**46**	2.26	31.5	18.1	0.33	0.33
1460	Gap	**246**	**74**	**75.8**	**938**	**106**	4.98	9.8	5.6	0.17	0.17
	Non-gap	**240**	**106**	**91.75**	**630**	**31**	4.79	13.4	7.7	0.20	0.20
1603	Gap	**257**	**52**	**66.1**	**537**	**96**	4.64	13.2	7.6	0.23	0.23
	Non-gap	**251**	**59**	**91.7**	**291**	**87**	3.52	17.4	10.0	0.29	0.29
1676	Gap	**263**	**42**	**17.2**	**1438**	**1262**	**6.80**	11.3	6.5	0.33	0.33
	Non-gap	**248**	**63**	**84.45**	**616**	**138**	**2.18**	15.4	8.9	0.28	0.28

Figure Legends

Figure 1. Hypotheses. We expected overall survival and growth to be highest in the middle of species' ranges, following classic fundamental niche theory and common assumptions made by natural resource managers, and hypothesized that climate (specifically, snow duration and growing season temperature) determines upper range limits of focal species, while competition drives lower range limits (A). We therefore expected that negative effects of competition on growth and survival would be strongest at low elevations (B). I also expected that origin population plays an important role in tree responses to climate, such that performance is highest when individuals are grown in their "home" elevation and its associated climate (C).

Figure 2. Study sites and experimental design. We established the experiment at seven different elevations on the south side of Mt. Rainier (A, map view, and B, profile view), and 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 (C, map view). 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. We transplanted seedlings (15 for *T. mertensiana*, 16 for *A. amabilis* and *T. heterophylla*) of the focal species into each plot.

Figure 3. Survival and growth of transplants was not highest in the middle of focal species' ranges. Observed species' ranges on Mt. Rainier are shown by gray shading, and points indicate average survival (A-C) and relative growth rates (D-F) of seedlings planted in the middle of their range, at upper and lower range limits, outside upper and lower range limits (across all treatments within each block). Error bars show standard error.

Figure 4. Competitive treatment affected survival and growth across species' ranges. For survival (A-C), the direction of effects varied with elevation: competition from understory (pale green), canopy (medium green), and both together (dark green) negatively affected survival across the range of all three species, except beyond upper limits, where canopy presence positively affected survival for *T. mertensiana* and *A. amabilis.* For relative growth rate (RGR, D-F), competition negatively affected growth across species' ranges, particularly from canopy trees and when both canopy and understory were present. Survival graphs show the difference in log-odds ratios for survival and RGR graphs show the difference between plots with competition compared to those with no competition present (gaps, with understory vegetation removed) at each elevation (i.e. the coefficient for "no competition" sites was subtracted from coefficients for understory and canopy effects). Survival coefficients came from best-fit binomial mixed effects models, while RGR coefficients were from linear mixed effects models, fit with elevation, canopy status, understory status, and all two-way interactions. (Best-fit

models for RGR did not include understory competition as an explanatory variable for any species, Tables 4-6.)

Figure 5. Origin population affected survival & growth, as it was included in nearly all best-fit models (except for survival of *T. heterophylla*), but effects varied by species and were not as great as effects from competition (Tables 1-6).

Figure 6. Microclimate and visible light varied with canopy competition, and may explain the facilitative effects of vegetation we observed. Snow duration increased with elevation, and was greater in canopy gaps compared with non-gaps (A), but was not affected by understory competition (Table 7). Growing degree days (GDD) were affected by both canopy (B) and understory vegetation (not shown, Table 8), but canopy effects were greater. As expected, canopy vegetation reduced light levels (C), as did understory vegetation (not shown, Table 9).

Figures

Figure 1.

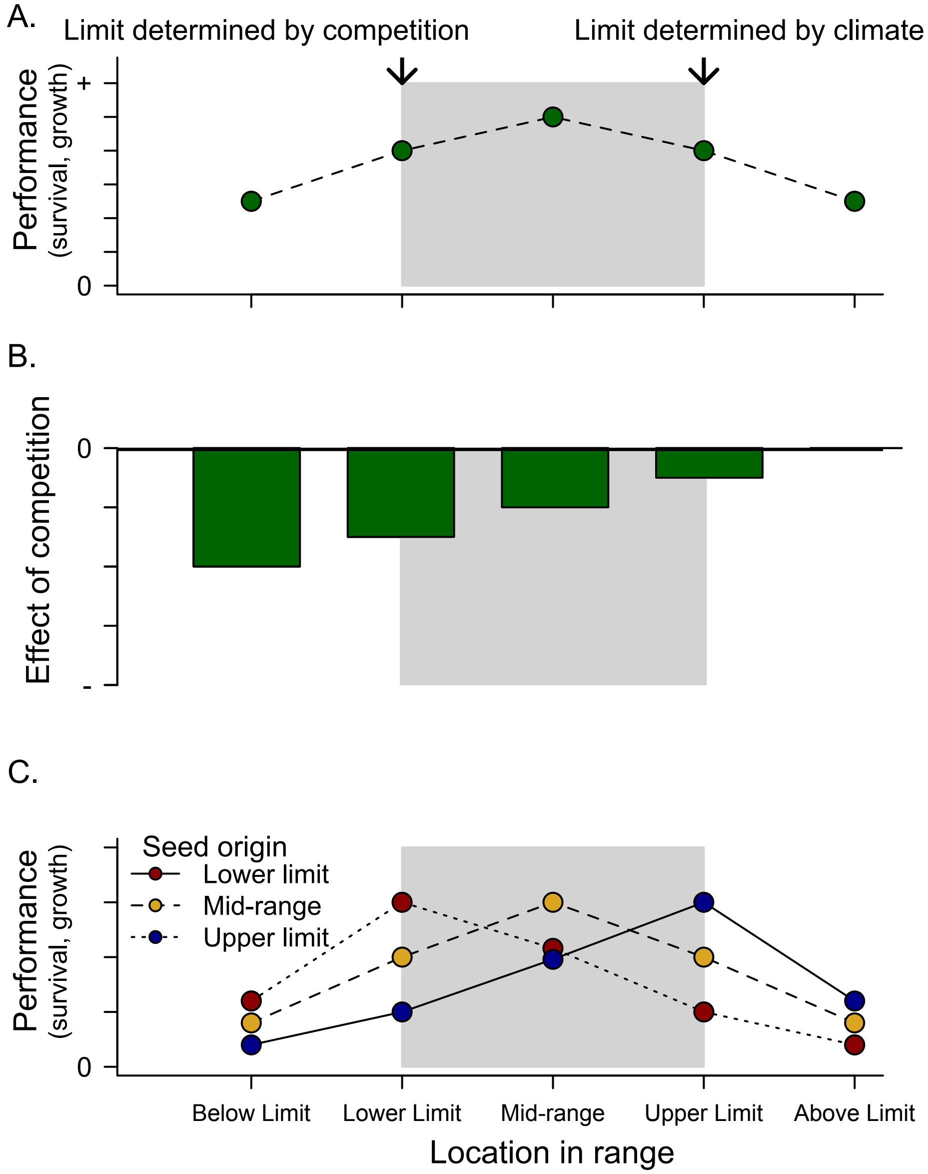


Figure 2.

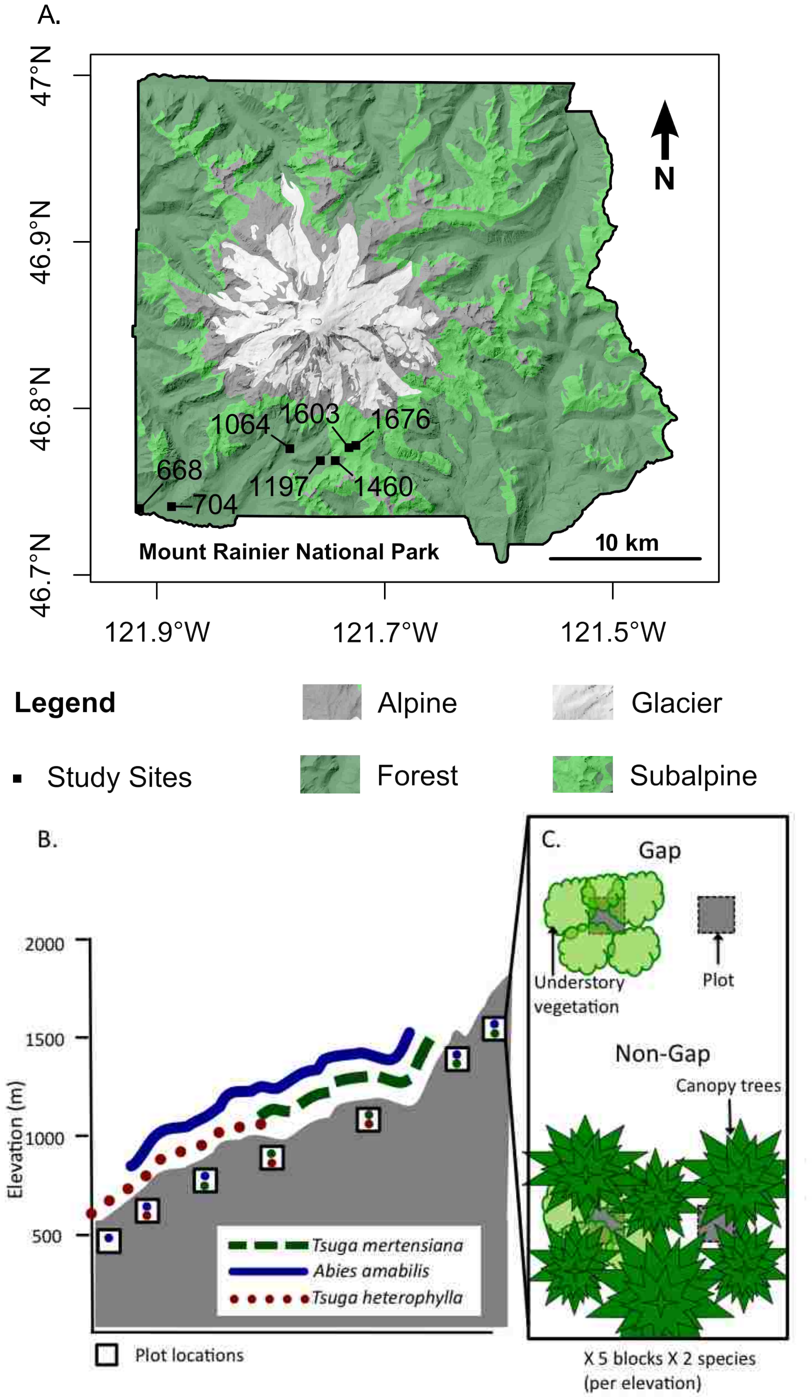

A.
47°N
46.9°N
46.8°N
46.7°N
121.9°W
121.7°W
121.5°W
N
1064
1603
1676
668
1197
1460
704
Mount Rainier National Park
10 km
Legend
Alpine
Glacier
Study Sites
Forest
Subalpine
B.
Elevation (m)
2000
1500
1000
500
Tsuga mertensiana
Abies amabilis
Tsuga heterophylla
Plot locations
C.
Gap
Understory vegetation
Plot
Non-Gap
Canopy trees
X 5 blocks X 2 species
(per elevation)

Figure 3.

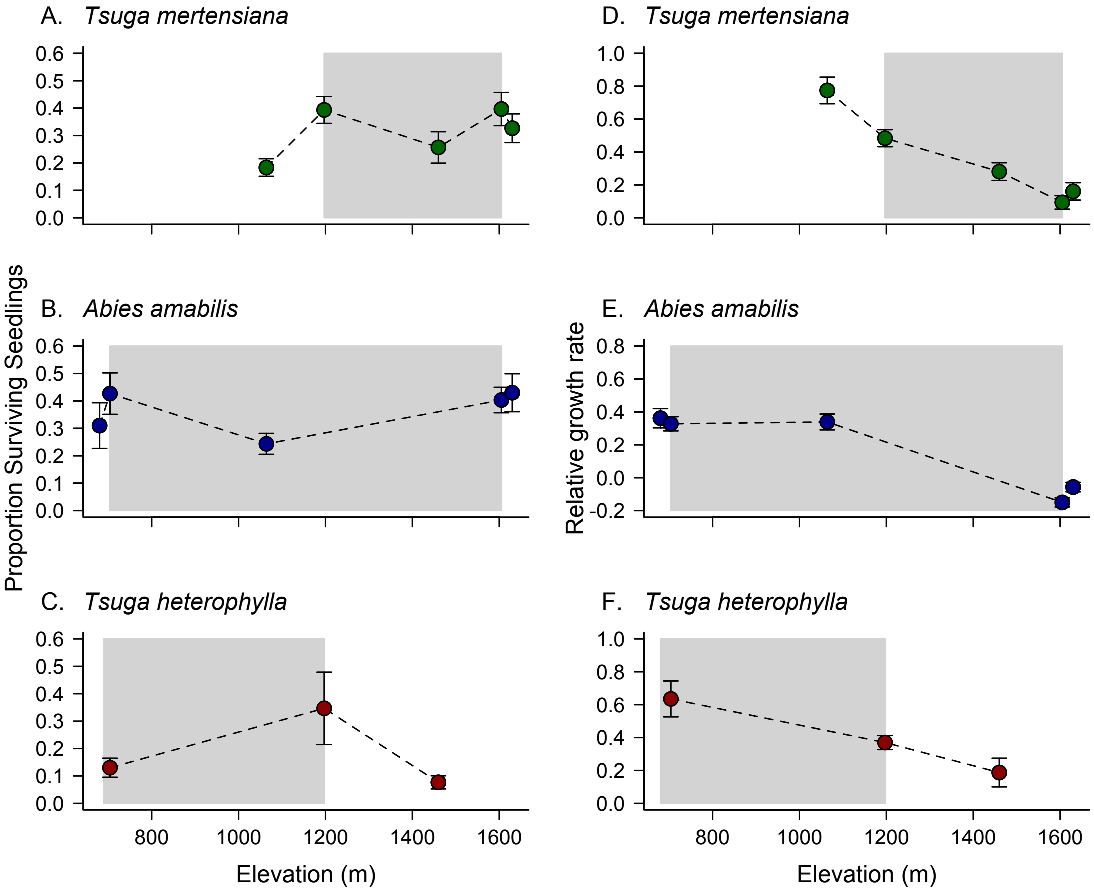

A. *Tsuga mertensiana*
B. *Abies amabilis*
C. *Tsuga heterophylla*
D. *Tsuga mertensiana*
E. *Abies amabilis*
F. *Tsuga heterophylla*
Proportion Surviving Seedlings
Relative growth rate
0.0
0.1
0.2
0.3
0.4
0.5
0.6
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
800
1000
1200
1400
1600
Elevation (m)
Elevation (m)

Figure 4.

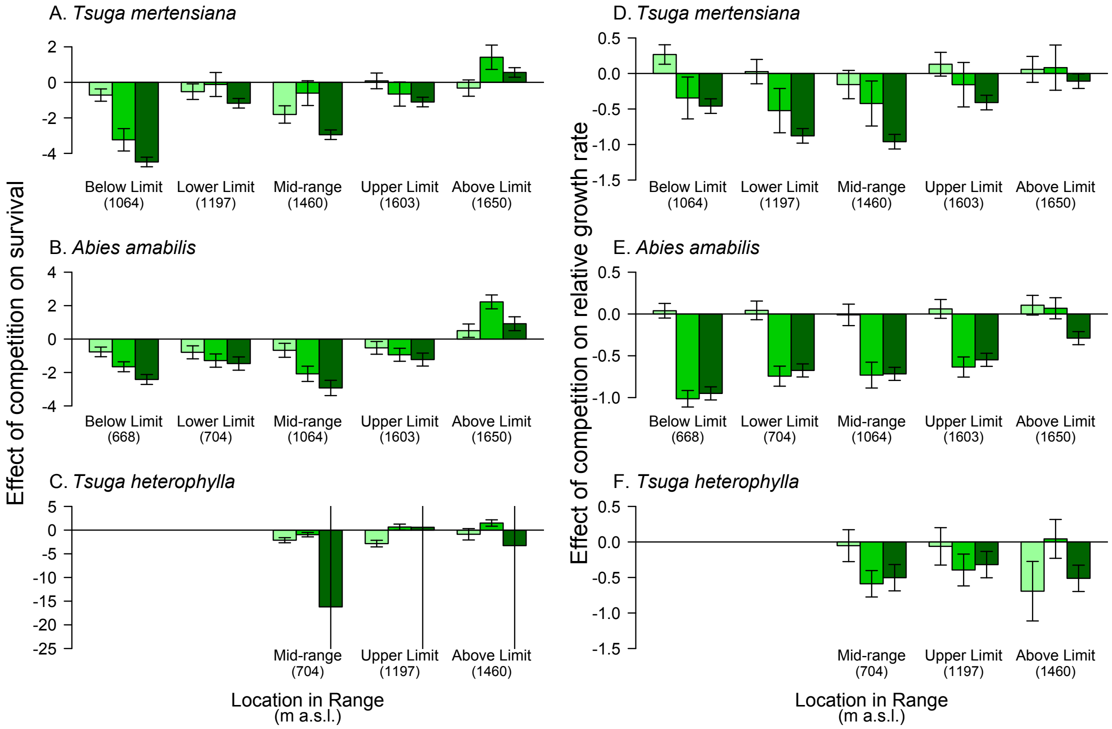

A. *Tsuga mertensiana*
2
0
-2
-4
Below Limit (1064)
Lower Limit (1197)
Mid-range (1460)
Upper Limit (1603)
Above Limit (1650)
B. *Abies amabilis*
4
2
0
-2
-4
Below Limit (668)
Lower Limit (704)
Mid-range (1064)
Upper Limit (1603)
Above Limit (1650)
C. *Tsuga heterophylla*
5
0
-5
-10
-15
-20
-25
Mid-range (704)
Upper Limit (1197)
Above Limit (1460)
Effect of competition on survival
Location in Range (m a.s.l.)
D. *Tsuga mertensiana*
0.5
0.0
-0.5
-1.0
-1.5
Below Limit (1064)
Lower Limit (1197)
Mid-range (1460)
Upper Limit (1603)
Above Limit (1650)
E. *Abies amabilis*
0.5
0.0
-0.5
-1.0
Below Limit (668)
Lower Limit (704)
Mid-range (1064)
Upper Limit (1603)
Above Limit (1650)
F. *Tsuga heterophylla*
0.5
0.0
-0.5
-1.0
-1.5
Mid-range (704)
Upper Limit (1197)
Above Limit (1460)
Effect of competition on relative growth rate
Location in Range (m a.s.l.)

Figure 5.

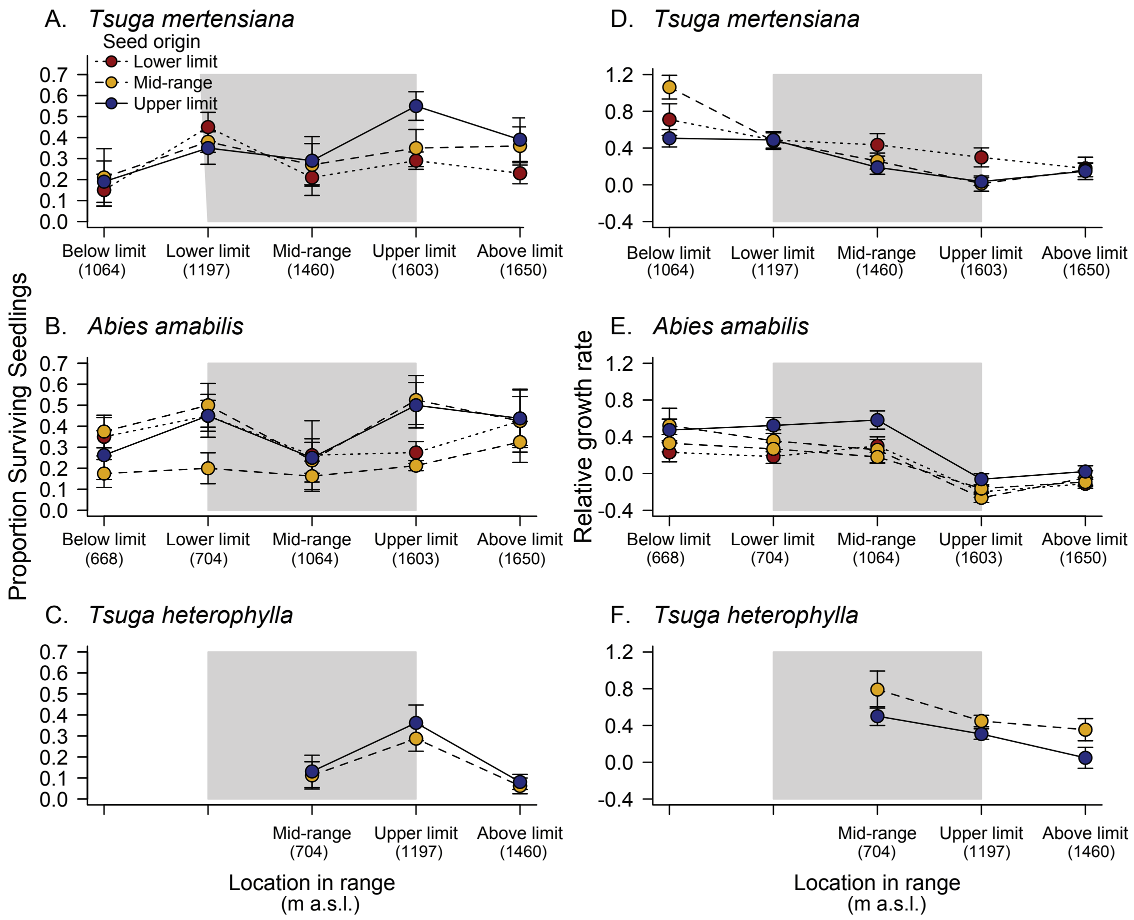
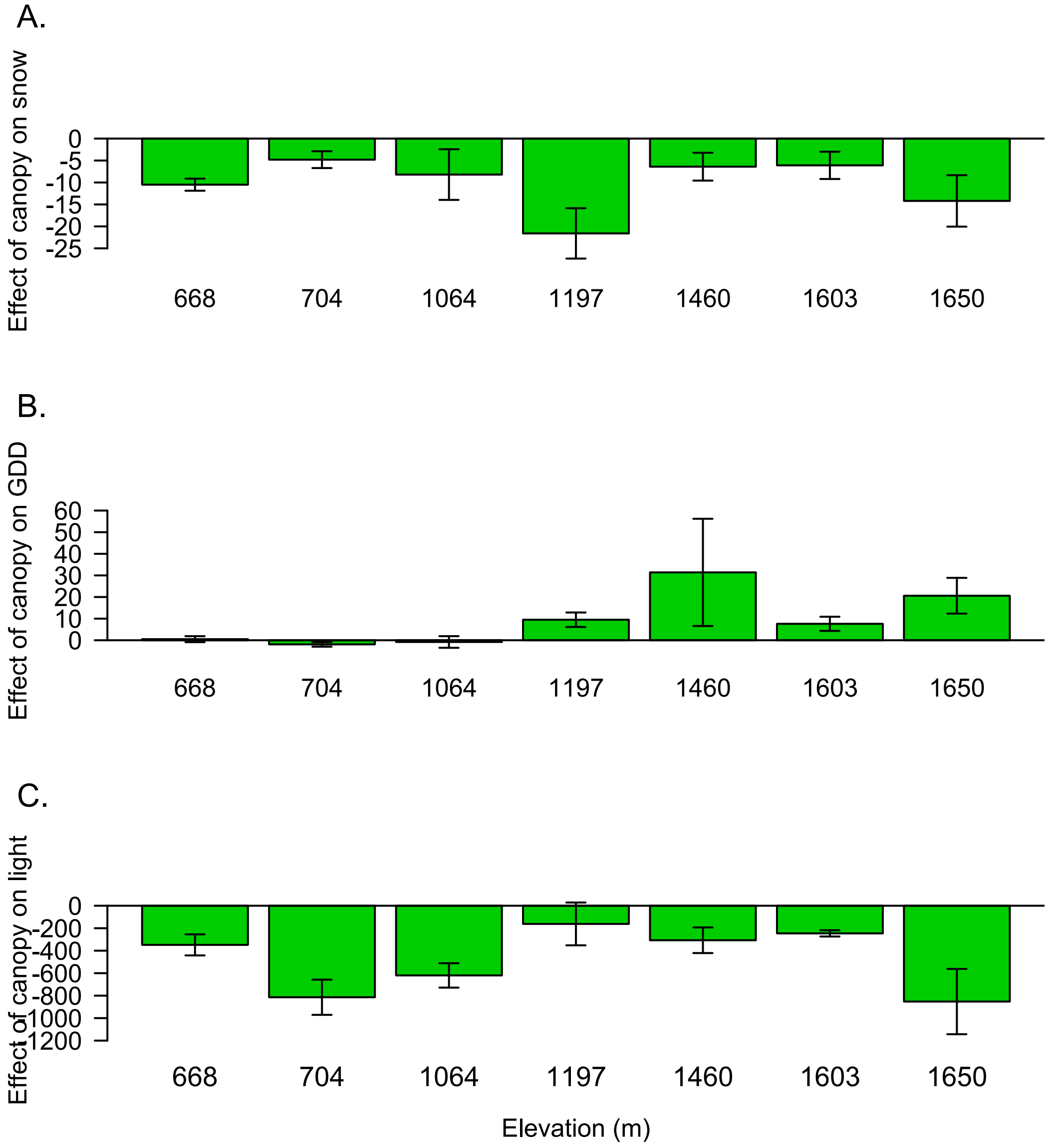

A. Tsuga mertensiana
Seed origin
Lower limit
Mid-range
Upper limit
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Below limit (1064)
Lower limit (1197)
Mid-range (1460)
Upper limit (1603)
Above limit (1650)
Proportion Surviving Seedlings
B. Abies amabilis
Below limit (668)
Lower limit (704)
Mid-range (1064)
Upper limit (1603)
Above limit (1650)
C. Tsuga heterophylla
Mid-range (704)
Upper limit (1197)
Above limit (1460)
Location in range (m a.s.l.)
D. Tsuga mertensiana
1.2
0.8
0.4
0.0
-0.4
Below limit (1064)
Lower limit (1197)
Mid-range (1460)
Upper limit (1603)
Above limit (1650)
Relative growth rate
E. Abies amabilis
Below limit (668)
Lower limit (704)
Mid-range (1064)
Upper limit (1603)
Above limit (1650)
F. Tsuga heterophylla
Mid-range (704)
Upper limit (1197)
Above limit (1460)
Location in range (m a.s.l.)

Figure 6.


A.
Effect of canopy on snow
0
-5
-10
-15
-20
-25
668
704
1064
1197
1460
1603
1650
B.
Effect of canopy on GDD
60
50
40
30
20
10
0
668
704
1064
1197
1460
1603
1650
C.
Effect of canopy on light
0
-200
-400
-600
-800
-1000
-1200
668
704
1064
1197
1460
1603
1650
Elevation (m)

CHAPTER 4

Conclusion: Synthesis and Implications

Taken together, results from Chapters 1, 2 and 3 provide valuable and unprecedented empirical data on the roles of climate and competition in determining the range limits of tree species on Mt. Rainier. No previous studies (to my knowledge) have similarly examined abiotic and biotic range limit determinants at both upper and lower limits (Sexton et al. 2009). Yet, such studies are critical for understanding a fundamental ecological question: why are species distributed as they are? In this time of rapid environmental change, studies such as these are also critical for accurately forecasting future range shifts due to anthropogenic climate change. In this section, we synthesize findings from all three chapters and describe implications of these findings for range limit determinants and for climate change-induced range shifts.

The Roles of Climate and Competition in Conifer Range Limits

Climate limits conifer performance at upper range limits on Mt. Rainier, suggesting climatic controls on upper range boundaries. Growth of saplings and adult trees was sensitive to heavy snowpack and cold temperatures at upper elevational limits, with low growth in cold and high snowpack years. Furthermore, adult growth was highly synchronized among individuals at high elevations – suggesting common constraints on growth that are likely climatic. Finally, seedling growth was likely also limited by climate, with strong reductions in height growth with increasing elevation (and snowpack). Seedling survival, however, was not strongly correlated with this elevational gradient.

At lower range limits, on the other hand, climate did not strongly limit performance for any species. Adult tree and sapling growth was comparatively poorly explained by climate at low elevations, compared with high elevations. Furthermore, annual adult growth at low elevations was poorly synchronized among individuals, indicating individual and neighborhood specific constraints on growth, rather than stand-level effects such as climate. Additionally, seedling growth was highest at lower and below lower range limits for all three focal species, and survival did not decline at and below lower range limits compared with other locations in the range. Our results therefore suggest that climate controls upper, but not lower, elevational range limits at Mt. Rainier.

Competition, not climate, appears to limit performance at lower range limits. While competition was important throughout the range for seedlings, competitive constraints on growth and survival were strongest at lower range limits. For saplings, competitive effects on growth were more important than for adults, but were equally important across their ranges. Thus, growth-competition relationships suggest that young trees (saplings and seedlings) are especially sensitive to competition, and that competitive effects are most limiting at low elevation range limits for seedlings.

Our results support a classic, but little tested, hypothesis: that biotic factors, such as competition, are more important where climates and other conditions are more benign (i.e. at lower range limits), while abiotic factors, such as temperature, control upper range limits (Connell 1961, Brown et al. 1996). Whereas previous tree studies have found patterns suggestive of this (e.g. Loehle 1998), to our knowledge our studies provide the first empirical evidence for tree species. Furthermore, our results bring to light a couple of additional important complexities in understanding range limit determinants:

1) Effects of climate and competition varied by life stage, suggesting that range limit determinants depend on the complex interplay of biotic and abiotic constraints that vary across species' lifespans. For example, adult trees were more sensitive to climate than saplings, while saplings were more sensitive to competition than adults. This finding underscores the need for biologists to study organisms across multiple life stages, rather than focusing on a single stage, in order to understand factors that determine species' distributions. As demonstrated by previous studies elsewhere in the world, individual tree species may persist via asexual reproduction through climates that limit sexual reproduction (Black and Bliss 1980). However, our studies lay the foundation for understanding the full range of an individual species' responses to climate.

2) Climate and competitive environment are not mutually exclusive range limit determinants. Rather, they interact and affect each other. For example, canopy presence was associated with reduced snow duration, and both canopy and understory presence were associated with increased growing degree days at highest elevations in our study. While climate appeared to limit growth and survival at upper range limits of our focal species, biotic interactions were also important. We saw evidence for facilitation at the highest elevation in our study, where survival was actually higher with understory and canopy presence.

3) Range limit determinants vary across species. We observed interspecific variation in the particular climate variables to which tree growth is sensitive, and in the strength of these growth-climate relationships. In this regard, our results confirm patterns noted by paleo-ecologists in the Pacific Northwest: species have responded individualistically to shifts in climate over the last 20,000 years (Dunwiddie 1986, Gavin et al. 2001, Gavin et al. 2013). In other words, whole communities did not remain intact and shift their ranges simultaneously, in concert with changing climates. Instead, the paleo-record exhibits combinations of species that differ from those observed today (Dunwiddie 1986, Gavin et al. 2001, Gavin et al. 2013).

Range Shifts Under Future Climate Change

Anthropogenic greenhouse gas emissions will cause global temperatures to continue rising at increasingly rapid rates over the next 100 years (IPCC 2007). In the Pacific Northwest, temperatures are expected to rise 3°C and snowpack is expected to decline more than 50% by the 2080s (Mote and Salathé 2009). These forecasted changes in climate are likely to have dramatic effects on tree performance at high elevations, given the strong effects of snow on tree growth and survival that we and others have observed (Franklin et al. 1971, Taylor 1995, Peterson et al. 2002, Rochefort and Peterson 1991) Warming temperatures and reduced snowpack and duration are likely to cause increased tree growth at upper limits of our focal tree species that reach tree line (~1650 m above sea level on the south side of Mt. Rainier). Increased growth is correlated with decreased mortality and increased reproduction in adult trees (Wyckoff and Clark 2002, Despland and Houle 1997). Thus, new establishment of individuals at high elevations will probably cause upward range shifts on the south side of Mt. Rainier. These upward shifts will likely occur slowly, however, since trees are long-lived on Mt. Rainier, and the adult stage appears to be the most climate-sensitive.

Climate change-induced shifts in range margins are likely to be less dramatic at low elevations, where climate does not appear to strongly limit growth and survival of focal tree species at any life stage. Shifts in tree distributions may depend more on altered disturbance regimes, pests, and pathogens, as well as competitive dynamics. How forecasted changes in climate will affect competitive environments is probably the least well understood. It is also possible that climate change will lead to increased frequency of disturbance events that alter competitive environments. For example, elsewhere in Washington state, disturbances from fire and insect (e.g., mountain pine beetle) outbreaks, which are both likely to increase with climate change, are expected to cause more dramatic changes to forest structure and composition than direct effects of warming on growth and survival (Littell et al. 2009).

Understanding and predicting future species' distributions are further complicated because anthropogenic climate change will likely cause other meteorological shifts besides simply increasing temperatures. For example, extreme high precipitation events are projected to increase in frequency, and seasonal precipitation cycles may move toward wetter autumns and winters and drier summers (Mote and Salathé 2009). Indeed, paleoecological studies confirm that climatic shifts over the past 20,000 years have resulted in combinations of meteorological factors that are not analogous to those observed today (e.g. Dunwiddie 1986, Prentice et al. 1991, Fall et al. 1995). Furthermore, we observed interspecific variation in the particular climate variables to which tree growth is sensitive, and in the strength of these growth-climate relationships. Thus, it is likely that future climate change will yield "no-analog" climates and ecological communities (Williams and Jackson 2007, Urban et al. 2012) .

Implications for Conservation and Future Research

Our results suggest that climate change will lead to increased growth and upward range expansion of Mt. Rainier's tree species. Thus, forests in the Park may be considered climate change "winners." The wildflower meadows and subalpine parkland that exist directly above these forests, on the other hand, may be climate change "losers." Trees may establish more rapidly into these meadows than the meadows can establish into the bare soil, rock, and ice that currently occur above them (Rochefort and Peterson 1996) . Furthermore, potential colonizable area decreases with elevation, due to the conical shape of mountains (Larsen et al. 2011). Potential declines in alpine and subalpine meadows pose a serious conservation concern, as these habits provide important ecosystem services including food sources for many animals, habitat for endemic species, and recreational opportunities (Franklin et al. 1971).

We found that at lower range limits of focal species, competition strongly affected performance, suggesting that biotic interactions will mediate climate change responses. How widespread is this patterns of biotic controls over lower limits and climatic controls over upper limits? More experimental studies of other biotic interactions (e.g. facilitation, consumption), diverse species, and widespread locations are necessary. These data should then be integrated into mechanistic models to enable more accurate forecasting of ecological effects of climate change. This would facilitate identification of "winners" and "losers" of climate change, which is critical for prioritizing conservation and natural resource management efforts.

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