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CLIMATE ISN'T EVERYTHING: COMPETITIVE INTERACTIONS
AND VARIATION BY LIFE STAGE WILL ALSO AFFECT RANGE
SHIFTS IN A WARMING WORLD[1]

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- *Premise of the study:* 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.
- *Methods:* 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 years of data) experienced by each individual.
- *Key results:* 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.
- *Conclusions:* 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.

Key words: climate change; competition; fundamental niche; migration; range shifts; realized niche.

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; Stott and 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 have demonstrated 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")
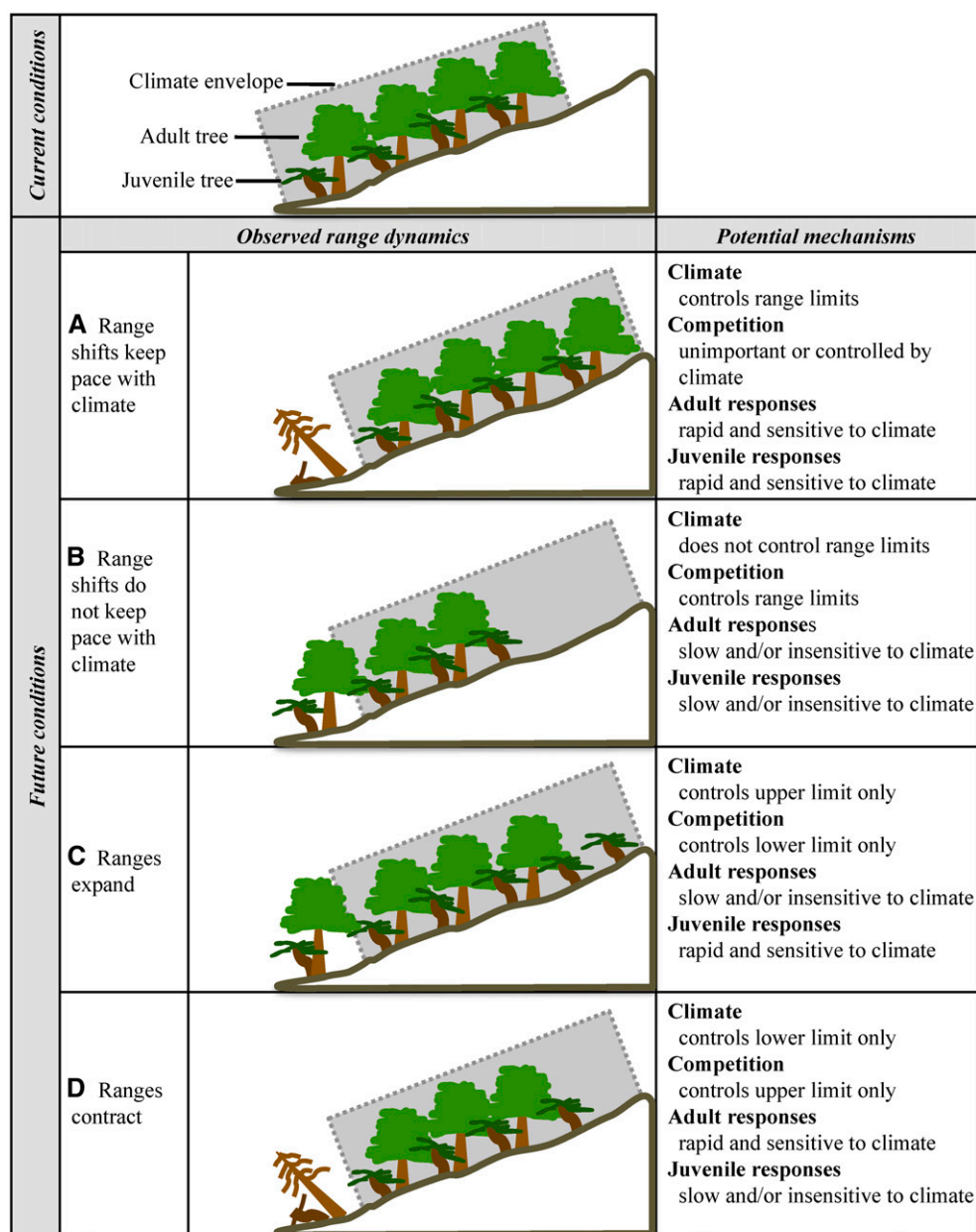
Fig. 1.   If climate alone does not determine range limits, anthropogenic warming could lead to complicated range shift dynamics. For example, assume that current observed species' ranges are at equilibrium with their climate niches (top panel). If climate alone controls range limits, species ranges 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).

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, see Supplemental Data with the online version of this article). 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) whether 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. 1).

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; Stott and 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. 2; 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 years 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 (online 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, Quebec City, 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

Effect of climate

Effect of competition

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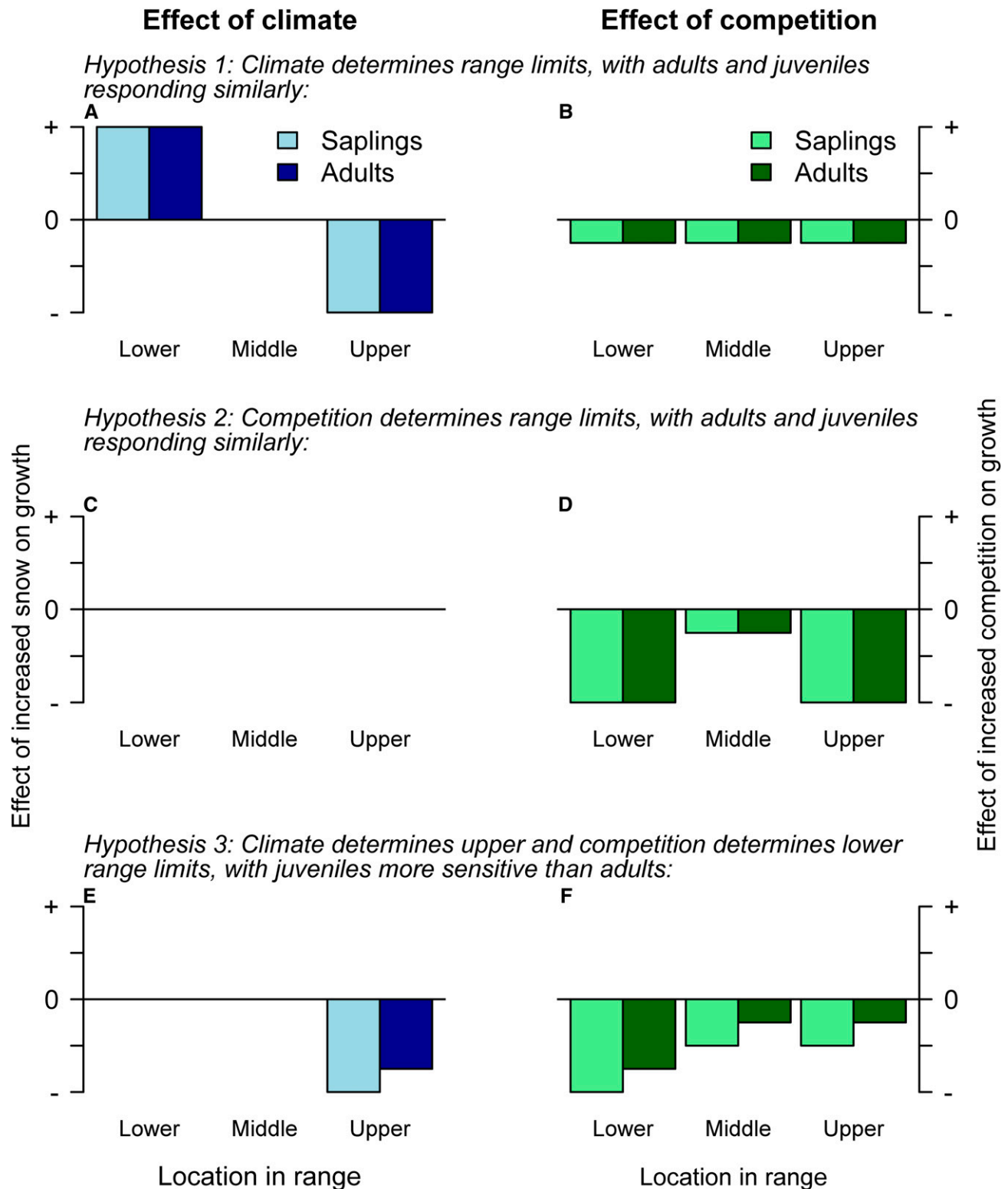

Fig. 2.   Hypotheses: Effects of climate and competition on species' performance should differ across ranges, depending on their relative importance in driving range limits. We expect that, if climate alone is important in driving species distributions and their responses do not vary by life history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

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 (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 (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 (Paramete–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 ($AIC_{Null} - AIC_{Best}$). 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).

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 1 to 10 m. Across all species, we compared model fit for each of these 10 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

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: $AIC_{Null} - AIC_{Best}$). 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 and mean annual temperature 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 | | | | | | | |
| | | Temperature (growing season) | | Temperature (dormant season) | | Precipitation (dormant season) | | Strength of climatic influence on growth | |
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,d]	**0.030**[c]	*0.036*[d,h]		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**[h]	−0.026[e]	2	4
	Mid (1064)					−0.007[e]		14	0
	Mid (1454)					**-0.019**[h]	**−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] Interaction term was not significant.
[e] Snow water equivalent (SWE)
[f] Snow duration (SNDR)
[g] Cumulative precipitation (PPT)
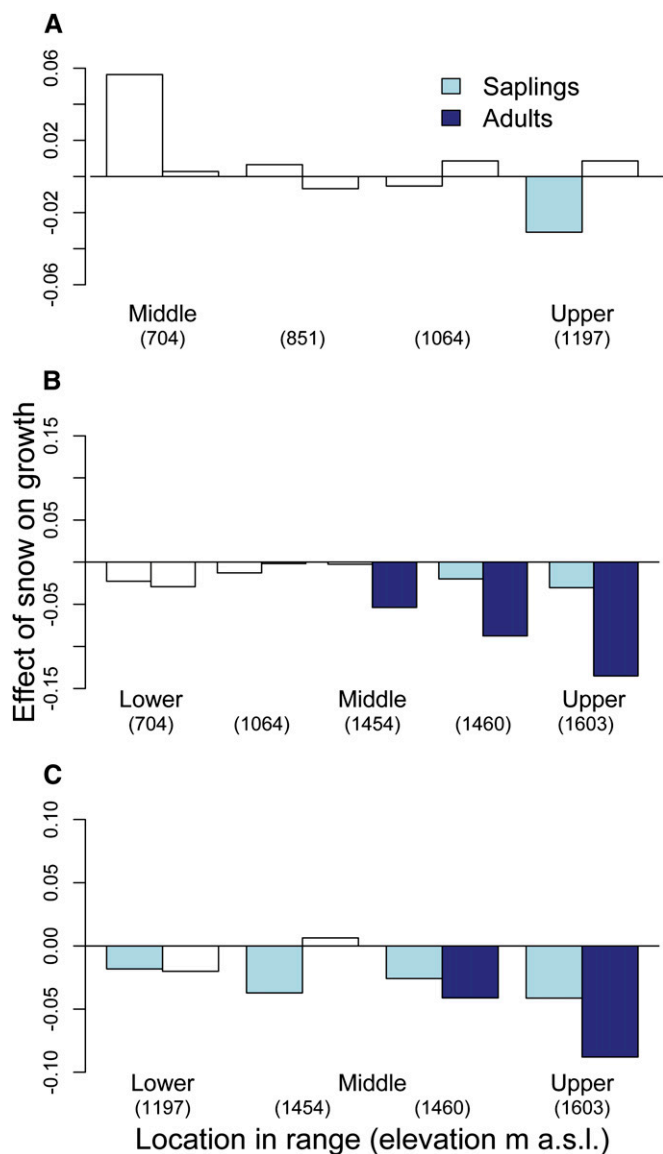[h] Dormant season precipitation (DPT)

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 ($P < 0.05$).

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

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. Significant effects ($P < 0.05$) are indicated by boldfaced text.

Species	Source of variation	Saplings				Adult trees			
		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	

elevations, e.g., Connell, 1961; Brown et al., 1996; Stott and 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 years 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., 2009). 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
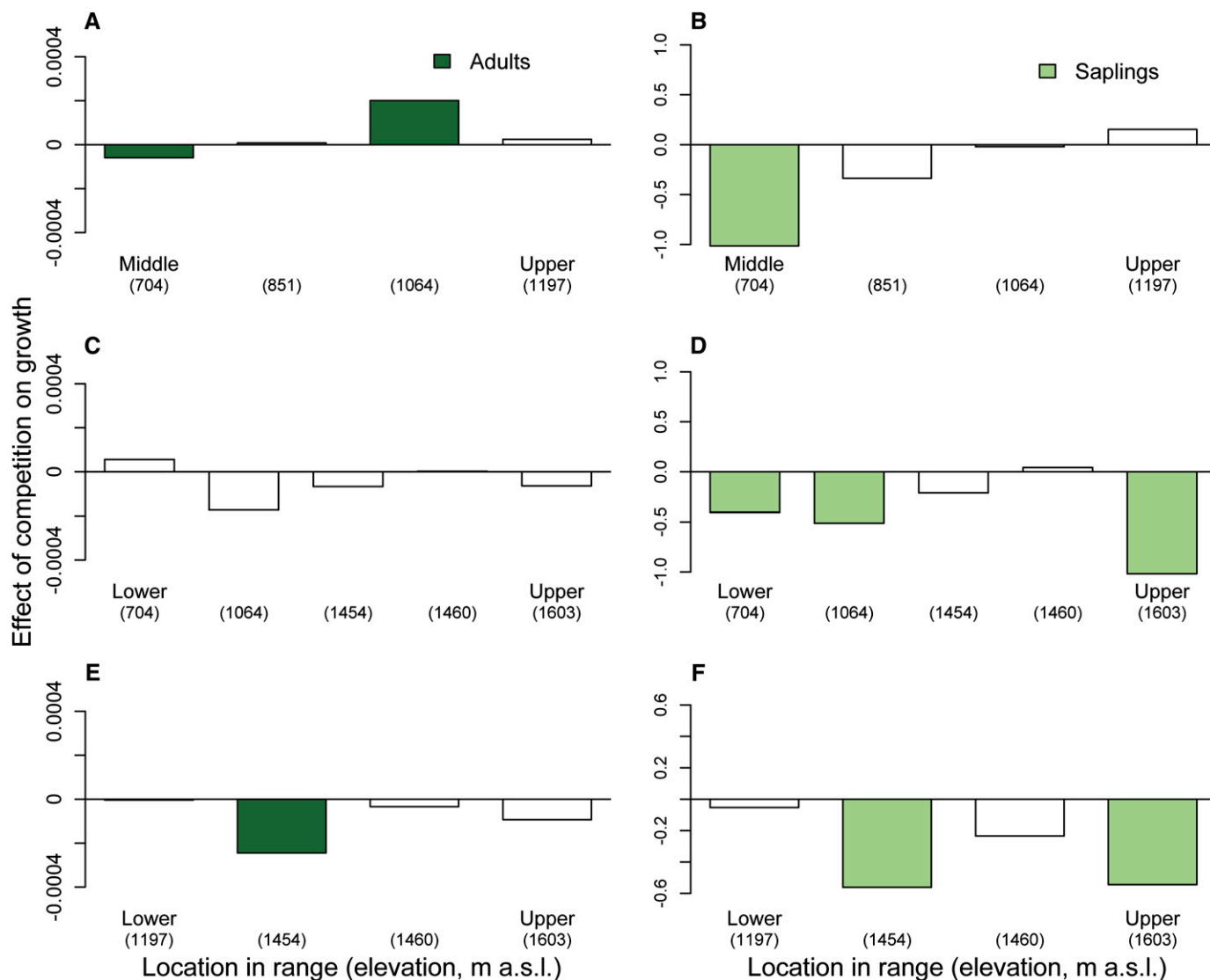
Fig. 4. Effects of competition differ by life stage and focal species. Across their ranges, focal species were generally negatively affected by competition at both life stages (Table 2). The exception to this was the adult stage of *Tsuga heterophylla* (A), which varied in its response to competitive 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.

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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