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The relative influences of climate and competition on tree growth along montane ecotones in the Rocky Mountains

Paige E. Copenhaver-Parry · Ellie Cannon

Abstract Distribution shifts of tree species are likely to be highly dependent upon population performance at distribution edges. Understanding the drivers of aspects of performance, such as growth, at distribution edges is thus crucial to accurately predicting responses of tree species to climate change. Here, we use a Bayesian model and sensitivity analysis to partition the effects of climate and crowding, as a metric of competition, on radial growth of three dominant conifer species along montane ecotones in the Rocky Mountains. These ecotones represent upper and lower distribution edges of two species, and span the

distribution interior of the third species. Our results indicate a greater influence of climate (i.e., temperature and precipitation) than crowding on radial growth. Competition importance appears to increase towards regions of more favorable growing conditions, and precise responses to crowding and climate vary across species. Overall, our results suggest that climate will likely be the most important determinant of changes in tree growth at distribution edges of these montane conifers in the future.

Keywords Distribution shift · Plant performance · Distribution edge · Bayesian model · Sensitivity analysis

Introduction

Rapid changes in temperature and precipitation over the next century are predicted to drive notable shifts in plant distributions (Parmesan 2006; McKenney et al. 2007; Kelly and Goulden 2008). Understanding the factors driving population performance at distribution edges will help to clarify expected species responses to future climatic conditions, as these edges likely represent either climatically induced physiological limitations or competition-related limitations on population growth that may vary under future climate (Stohlgren and Bachand 1997). While a number of studies have identified factors controlling species occurrence at distribution edges (e.g., Case et al. 2005; Morin et al. 2007; Barbeito et al. 2012; Schurr et al. 2012; Hargreaves et al. 2014), growth rates of individuals, which may be a better indicator of overall population performance, have received less attention (Lasky et al. 2013; Bin et al. 2015). Distribution shifts ultimately result from spatial and temporal variation in demographic rates (establishment, growth, mortality, dispersal) resulting from both abiotic and biotic

influences (Pulliam 2000; Knutson and Pyke 2008; Clark et al. 2011; Schurr et al. 2012; HilleRisLambers et al. 2013; Normand et al. 2014). While establishment and mortality events at distribution edges directly underlie species persistence and migration (Serra-Diaz et al. 2015), these demographic responses are often difficult to observe across broad regions without large-scale longitudinal studies (e.g., Clark et al. 2011). Growth, however, is more easily observed than alternative demographic rates and is strongly related to both fecundity and mortality risk through individual nutritional status (Kobe et al. 1995; van Mantgem et al. 2003; Wyckoff and Clark 2005; Clark et al. 2011). Growth can thus act as an integrative indicator of population performance that reflects sensitivity to both broad-scale abiotic drivers and local resource dynamics (McMahon et al. 2010; Clark et al. 2011). Additionally, growth responds rapidly to climate change, allowing growth rates to act as a particularly useful indicator of population sensitivity to climate change (McMahon et al. 2010; Renwick and Rocca 2015).

Both climate and competition have been recognized as important controls on plant growth, though their relative importance at distribution edges remains uncertain (Normand et al. 2014). Climate has been consistently shown to limit growth of temperate trees at range and distribution edges (e.g., Grabherr et al. 1994; Cannone et al. 2007; Morin et al. 2007; Barbeito et al. 2012; Case and Duncan 2014), though its influence has rarely been evaluated relative to that of competition (but see Ettinger et al. 2011; Ettinger and HilleRisLambers 2013). Where relative effects have been evaluated, the focus has been primarily on edges occurring at treeline (Case and Duncan 2014), and rarely for distribution edges that occur within closed-canopy forests (but see Ettinger et al. 2011, 2013). The importance of climate relative to competition is generally expected to increase in regions of high abiotic stress (Tilman 1982; Keddy 1989; Gaudet and Keddy 1995), and several empirical studies have corroborated this theory (Coomes and Allen 2007; Meier et al. 2010; Kunstler et al. 2011; Gómez-Aparicio et al. 2011; Hargreaves et al. 2014). Within closed-canopy forests, competition is expected to be greater than at forest edges owing to dense tree cover, and dense canopies may buffer climate effects (Holman and Peterson 2006; Ettinger et al. 2011; HilleRisLambers et al. 2013; Dobrowski et al. 2015). Distribution edges within closed canopies are encountered by many species in mountain environments, and resolving drivers of growth variation at such edges is crucial to understanding population and distribution responses to climate change.

In this study, we use a Bayesian model to directly quantify the contributions of climate (i.e., temperature and precipitation) and a metric of competition (i.e., crowding) to

tree radial growth for three abundant conifer species [*Pinus contorta* var. *latifolia* (Engelm.), *Pinus ponderosa* var. *scopulorum* (Engelm.), *Pseudotsuga menziesii* var. *menziesii* (Mirb.)], across closed-canopy ecotones in the Central and Northern US Rocky Mountains. These ecotones represent upper distribution edges of *Pinus ponderosa* and lower distribution edges of *Pinus contorta*. *Pseudotsuga menziesii* co-occurs with both *Pinus* species at mid-elevations, and thus has its distribution interior in these ecotone regions (Peet 1981; Sherriff and Veblen 2006; Schoennagel et al. 2011). The focal species have been studied extensively across our study region, and previous studies have identified distinct life history traits that may influence each species' sensitivity to climate and competition. In the Central and Northern Rocky Mountains, *Pinus contorta* and *Pinus ponderosa*, both relatively shade-intolerant species, regenerate rapidly following disturbance (Peet 1981; Burns and Honkala 1990; Hood et al. 2012). Growth of *Pinus contorta* is thought to be regulated by high intraspecific competition in dense, regenerating stands (Day 1972; Peet 1981; Knowles and Grant 1983; Burns and Honkala 1990; Copenhaver and Tinker 2014). *Pinus ponderosa* growth has been found to be highly correlated with temperature (Carnwath et al. 2012), as it can withstand a broad range of precipitation conditions due to deep tap roots (Burns and Honkala 1990; Nystrom Mast et al. 1998). *Pseudotsuga menziesii* is a moderately shade-tolerant species that generally establishes in canopy gaps (Burns and Honkala 1990; Schoennagel et al. 2004; Keeling et al. 2006; Devine and Harrington 2008; LeMay et al. 2009; Briggs et al. 2012) and prefers mid-elevation habitats characterized by moderate temperature and precipitation (Sterba and Monserud 1995; LeMay et al. 2009). *Pseudotsuga menziesii* tends to act as a later-seral species in mid-elevation forests in this region, replacing both *Pinus ponderosa* and *Pinus contorta* with sufficient time between stand-replacing fire events (Peet 1981; Burns and Honkala 1990; Scott 1998; Baker et al. 2007).

Our objectives were to:

1. Quantify the relative influences of climate and crowding on tree radial growth along closed-canopy ecotones for our focal species.
2. Assess variation in the relative importance of competition among species and across climate gradients that are relevant in the context of climate change.

We hypothesize that climate effects will be greater than the effects of crowding at distribution edges. Further, we hypothesize that the importance of competition among individuals of each species will increase towards more favorable climatic conditions.

Materials and methods

Field data

Tree radial growth data were collected from a series of plots nested within three sites in the Central and Northern US Rocky Mountains during June and July 2014. Sampling sites were selected to capture the range of conditions across which the focal species co-occur, and were located in the montane zones of the Bighorn National Forest, Wyoming, Bitterroot National Forest, Montana, and Ashley National Forest, Utah. All sites are characterized by elevational zonation of dominant tree species with mixed stands occurring in regions of overlap. Detailed site descriptions can be found in Online Resource, Appendix S1.

At each study site, five to six sampling transects were established to encompass the shift in dominant vegetation from upper-elevation *Pinus contorta* stands to lower-elevation *Pinus ponderosa* stands. While our approach of sampling across only one ecotone type does not allow us to evaluate factors controlling growth at upper and lower distribution edges of each individual species, it does enable us to draw general inference as to the relative influences of climate and crowding on growth at closed-canopy distribution edges without magnifying the influence of unmeasured factors that may be included by sampling across a broader elevational range (e.g., additional species, edaphic factors, radiation, microclimate). This asymmetric sampling design is consistent with similar studies (Ettinger et al. 2011; Ettinger and HilleRisLambers 2013). Transect number was limited by availability of *Pinus contorta*—*Pseudotsuga menziesii*—*Pinus ponderosa* ecotones in each site. Each

transect consisted of three 20 × 20-m (0.04-ha) sampling plots spaced equidistantly. Transect length varied according to the length of the transition zone between dominant over-story species.

To estimate the impact of neighborhood basal area on tree radial growth, we collected neighborhood data for three mature trees of each represented focal species in each plot. Each focal tree was measured for diameter at breast height (DBH; 1.37 m) and cored to the pith. Within an 11-m radius of each focal tree, DBH was recorded for all neighboring trees belonging to one of the three focal species. An 11-m neighborhood radius is consistent with recommendations from other neighborhood studies conducted within montane forests of the Rocky Mountains (Woodall et al. 2003; Contreras et al. 2011), and corresponds with roughly 3.5 times the average crown radius, or the estimated zone of competitive influence (Lorimer 1983). Other species such as *Populus tremuloides* and *Abies lasiocarpa* were present in several plots, but made up only a negligible portion of neighborhood basal area and were thus ignored during data collection.

according to standard procedures, and ring widths were measured using an ACU-RITE Velmex tree-ring measurement system (Heidenhain, Schaumburg, IL). Cores were visually cross-dated (Stokes and Smiley 1968), and increments from the most recent 10 years of growth (2004 up to and including 2013) were averaged to relate mean annual growth increment to climate and neighborhood competition (i.e., crowding). Only the most recent 10 years of data were retained because neighborhood data was not deemed to be reliable beyond this range; unknown growth, regeneration and mortality events occurring within each neighborhood could have resulted in substantial temporal variation in neighborhood basal area beyond the temporal range included in this study. In total, 172 tree cores and corresponding neighborhoods were retained for analysis: 63 of *Pinus contorta*, 49 of *Pinus ponderosa*, and 60 of *Pseudotsuga menziesii*.

Climate data

Climate data for each plot were extracted from the ClimateWNA database. ClimateWNA provides high-resolution climate estimates suitable for integration with our plot-level data by downscaling monthly parameter elevation regression on independent slopes model (PRISM) data from Western North America to specific point estimates using bilinear interpretation (Wang et al. 2012). As a major aim of this study was to quantify changes in growth across environmental gradients that are relevant in the context of climate change, we selected climate variables that have, in some cases, already changed substantially from long-term mean values, and are forecast to continue to change in the future (Dobrowski et al. 2013; IPCC 2013). Initial variables selected were mean annual temperature (MAT), mean warmest month temperature (MWMT), mean annual precipitation (MAP), mean annual summer (May–September) precipitation (MSP), summer heat-moisture index [$SHM = ((MWMT)/(MSP/1000))$], degree-days above 5 °C (growing degree-days; DD5), frost-free period (FFP), and precipitation as snow (PAS). Climate variables were averaged across the last 10 years of tree growth to remain consistent with mean radial increment data. All selected temperature variables were found to be highly correlated with one another (Pearson's $r > 0.7$), as were all precipitation variables, necessitating that only one variable from each group be included in the radial growth models. We evaluated each pair of uncorrelated temperature and precipitation variables separately and retained the best-fitting models (see "Radial growth model"). While climate may have an indirect effect on crowding by influencing competitor density, neighborhood basal area in this study was not significantly correlated with any climate variable [Pearson's $r < (0.5)$]. Using averaged values likely contributed

to the decoupling of climate and crowding in our data. Due to this lack of correlation as well as model limitations associated with sample size (see "Radial growth model"), the effects of crowding and climate were evaluated independently.

Radial growth model

Mean radial growth of individual trees over the past 10 years was modeled as a function of climate and basal area of competitors using a Bayesian regression model adapted from Kunstler et al. (2011). Tree size and age were initially included as model covariates, but showed insignificant effects for all species and were thus removed from the final models. A separate model was fitted for each of the focal species. Models with both linear and nonlinear climate effects were evaluated for convergence and fit, and models with linear climate effects (Eq. 1) were retained for all subsequent evaluation and analysis. While plant species have been shown to respond in a Gaussian-like fashion to gradients of temperature and precipitation (Boucher-Lalonde et al. 2012), our data span only a portion of each species' climatic tolerance. As such, only a localized region of each Gaussian-like response is captured, which may be adequately represented by a linear function. Interaction terms were evaluated in initial model formulations (temperature \times precipitation, climate \times competition), but inclusion of additional terms prevented convergence with the limited sample size of this data set, thus necessitating a simpler model form. The final models regress

mean radial growth (G ; mm year⁻¹) for focal tree i in plot p and transect t against climate (T and P), and an index of neighborhood crowding (neighborhood index; NI):

$$G_{i,p,t} = \frac{\alpha_t + \beta_1 T_p + \beta_2 P_p}{(1 + \frac{NI_i}{\beta_3})^{\beta_4}} \quad (1)$$

α , β_1 , β_2 , β_3 , and β_4 are parameters to be estimated. α is a random effects term that accounts for transect-level variability in abiotic conditions left unexplained by other model parameters. β_1 and β_2 describe the effects of temperature (T_p) and precipitation (P_p), respectively, at each plot. Crowding is represented by a semi-distance-independent neighborhood index (Ledermann 2010), NI_i (Eq. 2). Neighborhood indices have a rich history of use for evaluating the effects of competition on tree growth (e.g., Bella 1971; Hegyi 1974; Lorimer 1983; Weigelt and Jolliffe 2003; Canham et al. 2004; Contreras et al. 2011; Baribault and Kobe 2011; Aakala et al. 2013). These indices relate neighbor tree size and proximity to focal tree growth, with the assumption that neighboring trees could be affecting

one another through both below- and aboveground mechanisms of competition (Larocque 2002; Woodall et al. 2003; Canham et al. 2004). While resource heterogeneity can contribute to considerable variation in precise competition outcomes, neighborhood indices reflect the general relationship between resource consumption and plant size (Weiner 1985; Weiner and Thomas 1986; Casper and Jackson 1997; Tilman 1982; Weigelt and Jolliffe 2003). The neighborhood index used in this study is a function of the summed basal area (BA; m²) of all trees within an 11-m radius of the focal tree:

$$NI_i = \sum_{j=1}^n BA_{1,j} + BA_{2,j} + BA_{3,j} \quad (2)$$

where 1, 2 and 3 represent the focal species *Pinus con-torta*, *Pinus ponderosa* and *Pseudotsuga menziesii*, respectively. An 11-m neighborhood radius is consistent with the estimated zone of competitive influence, or roughly 3.5 times the average crown radius (Lorimer 1983; Contreras et al. 2011). We selected BA as our metric of competitor size because it has been demonstrated to scale more directly with the competitive effect of a neighbor than DBH (Canham et al. 2004). A pooled neighborhood index that includes all species of neighbors was necessary to reduce model dimensionality and allow for convergence. This approach does not allow us to directly evaluate the effect of interspecific versus intraspecific crowding, but does enable us to compare the overall effect of crowding to climate effects.

The growth model assumes a logistic relationship between neighborhood basal area (NI) and tree radial growth. In this specification, β_3 adjusts the intercept of the logistic relationship and β_4 represents the slope, which can be used to understand the strength of the neighborhood effect relative to climate effects. A positive value for β_4 represents a negative relationship between tree radial growth and neighborhood basal area, while a negative value represents a positive relationship.

All explanatory variables were re-scaled by dividing by their ranges prior to parameter estimation to aid parameter interpretation and improve model convergence. Radial growth ($G_{i,p,t}$) was modeled as normally distributed, with mean equal to the regression equation and a variance of ε , an estimated parameter that represents the process error. ε was characterized by an inverse gamma distribution [\sim IG(0.1, 10)], selected because of its conjugacy with the normal distribution. The transect effect parameter (α) was distributed normally with a prior mean of zero and variance (τ). τ was modeled with a gamma distribution and informative priors. All β parameters were distributed normally with uninformative priors centered on zero with large variance, \sim N(0|100).

Posterior parameter distributions were estimated using Markov Chain Monte Carlo methods within the JAGS 3.13 interface for R (Plummer 2014). Each model was run for 50,000 iterations with a burn-in period of 2000 iterations to achieve convergence. Iterations were thinned to every 100th value for post-processing. Each model was run with four chains, and convergence was assessed visually.

Separate models were fitted with different pairs of temperature and precipitation variables. The evidence for variable selection was evaluated using posterior predictive loss (PPL), a model fit criterion. This criterion accounts for goodness-of-fit and penalizes for complexity while avoiding specification of the number of parameters, which is often difficult for hierarchical models (Gelfand and Ghosh 1998). The model with the lowest posterior predictive loss score for each species was selected for subsequent analysis. Model bias was assessed by calculating the slope of the relationship between observed and fitted values; a value of 1 indicates no bias.

Additional analyses

We performed a sensitivity analysis to determine how model parameters vary in their effects on tree radial growth. Sensitivity analyses are aimed to demonstrate how model output varies across a range of plausible parameter values corresponding with uncertainty in parameter estimates (Saltelli 2005; Larocque et al. 2008; Crosetto and Tarantola 2001). Parameter uncertainty arises from variability in data, and in this way, the sensitivity analysis propagates data variability and parameter uncertainty through to model output. This approach allows for more meaningful interpretation of the influences of individual parameters than relying on a comparison of parameter point estimates, which may be misleading for poorly constrained parameters (Larocque et al. 2008; LeBauer et al. 2013). Following the methods for Bayesian sensitivity analysis outlined by LeBauer et al. (2013), we calculated sensitivity as the derivative of the model output with respect to each individual parameter. Parameters were evaluated at seven quantiles from each parameter's posterior distribution corresponding with the posterior mean, the 2.5 % quantile, the 97.5 % quantile, and quantiles corresponding with 1, 2, and 3 SDs on the standard normal distribution. This range was selected to represent the range of plausible values for a given parameter. All other parameters were held constant at their posterior mean while a single parameter was perturbed. The derivative of each relationship between parameter values and model output was used to approximate the model sensitivity to a given parameter. Because parameters were fitted based on re-scaled variables, sensitivity can be compared across parameters (Saltelli 2005). High parameter sensitivity is interpreted as representing a larger influence of that

parameter on variation in radial growth, and low sensitivity as a smaller influence (Larocque et al. 2008). High sensitivity may arise either as a result of true variability in parameter effects or from poor characterization of a parameter by insufficient or inadequate data.

Model output from the best models for each species was used to evaluate relationships between tree growth and competition importance across the climate gradients encountered in the study region. Fitted radial growth models were used to estimate competition importance for each focal tree. A standard index of competition importance was used, which calculates competition importance as a function of the relative difference of tree growth in the absence and presence of neighbors (Eq. 3; Welden and Slauson 1986; Brooker et al. 2005; Kunstler et al. 2011):

$$C_{\text{imp}} = \frac{G_0 - G_c}{\max(G_0) - \min(G_c)} \quad (3)$$

where G_0 represents the predicted growth in the absence of competitors (i.e., NI was set at zero to predict G_0) and G_c represents the predicted growth with competitor basal area equal to that observed for each focal tree. Both G_0 and G_c are calculated with temperature and precipitation equal to observed values, allowing G_0 and G_c to vary across climate gradients. It should be noted that our data set included a number of individuals with low crowding, but no individuals for which neighbors were absent. Our G_0 values are thus predicted from the radial growth model and represent an extrapolation from our data. G_c values are also predicted from the model, but fall within the range of sampled values. Our use of modeled G_0 and G_c is consistent with standard applications of these metrics (e.g., Canham et al. 2004; Kunstler et al. 2011). Competition importance for each species was regressed across climate gradients using linear models. Predicted growth in the absence of competition (optimal growth) and modeled growth with observed neighborhood indices (realized growth) were also regressed against climate variables using linear models to assess growth rankings and the effect of crowding on growth across climate gradients.

Results

Model fit and sensitivity

For all species, including MSP and DD5 improved model fit over all other combinations of uncorrelated precipitation and temperature variables (Table 1). Predicted versus observed growth relationships showed little bias in the models, though *Pseudotsuga menziesii* growth was predicted with substantially more bias than either *Pinus contorta* or *Pinus ponderosa* growth.

Table 1 Posterior predictive loss (*PPL*) and bias values evaluating all pairs of uncorrelated temperature and precipitation variables in the linear climate effects model (Eq. 1)

Species	MSP, FFP		MSP, MAT		MSP, MWMT		MAP, DD5		MSP, DD5	
	PPL	Bias	PPL	Bias	PPL	Bias	PPL	Bias	PPL	Bias
<i>Pinus contorta</i>	222.17	0.871	215.29	0.875	213.27	0.863	213.11	0.866	209.59 ^a	0.865 ^a
<i>Pinus ponderosa</i>	— ^b	— ^b	156.53	0.893	159.49	0.893	159.58	0.900	153.45 ^a	0.890 ^a
<i>Pseudotsuga menziesii</i>	254.74	0.711	256.74	0.710	256.2	0.727	263.33	0.718	254.01 ^a	0.712 ^a

PPL and bias are shown for the reduced model form, which eliminated size and age effects due to their insignificance

MSP Mean annual summer (May–September) precipitation, FFP frost-free period, MAT mean annual temperature, MWMT mean warmest month temperature, DD5 degree-days above 5 °C (growing degree-days)

^a Values for selected models (lowest PPL)

^b Models that failed to converge

For all species, mean parameter values showed a positive relationship between growing season temperature (β_1) and growth ($G_{i,p,t}$), and a negative relationship between summer precipitation (β_2) and growth (Table 2). When mean climate effects were evaluated independently with all other parameters and variables held constant at their mean values, growth varied more with temperature than with precipitation (Fig. 1b, c). *Pinus contorta* responded most strongly to both temperature and precipitation gradients, followed by *Pinus ponderosa* and *Pseudotsuga menziesii* (Table 2; Fig. 1b, c). In all cases, the competition parameter, β_4 , was positive, indicating a crowding effect of neighboring trees and a reduction in focal tree growth as neighborhood basal area increased. Both crowding parameters together (β_3 , β_4) predict substantial decreases in growth with increasing NI for all species (Fig. 1a). The mean transect effects term (α) was characterized by a broad posterior distribution and high variance (τ). Random effects for individual transects varied between positive, negative and insignificant values with no discernable trend. Overall, parameter values showed similar trends for all three species.

The sensitivity analysis revealed a higher sensitivity of modeled radial growth variation of all species to the climate parameters (β_1 , β_2) and a lower sensitivity to crowding parameters (β_3 , β_4 ; Table 3). Sensitivity to α , which represents transect effects not accounted for by other parameters, was also greater than sensitivity to either crowding parameter. Sensitivity to crowding parameters was notable for all species, yet substantially lower than sensitivity to climate parameters. Because variance in covariates differs for each species, sensitivity values cannot be compared across species.

Competition importance

Across all climate gradients, competition importance was generally low (<50 %) and invariant for both *Pinus contorta* and *Pinus ponderosa* (Fig. 2a, b). *Pinus contorta* competition importance showed no significant linear

any climate gradient (linear model $p > 0.05$), while *Pinus ponderosa* competition importance declined slightly with increasing MAP and PAS. In contrast, *Pseudotsuga menziesii* competition importance varied significantly across all climate gradients analyzed (linear model $p < 0.05$), increasing with temperature (DD5, MAT) and decreasing with increasing precipitation (MSP, MAP, PAS; Fig. 2c). Overall, competition importance was highest for *Pseudotsuga menziesii* in warmer, drier regions, while competition importance for *Pinus ponderosa* was slightly higher in drier regions.

Potential versus realized growth

Across all species and climate gradients, predicted optimal growth (growth in the absence of crowding) was generally higher than modeled realized growth in the presence of observed crowding, providing evidence for the role of neighboring trees in limiting focal tree growth (Fig. 3). For all three species, both realized and optimal growth generally increased with temperature and declined with precipitation. For *Pinus contorta* (Fig. 3a), both optimal and realized growth were greatest in warmer, drier regions. Optimal growth was significantly greater than realized growth across the range of climate conditions, except for under very low MSP. On average, *Pinus contorta* realized growth was reduced by 45 % from optimal growth.

Pinus ponderosa growth varied across gradients of DD5, MAT, MAP and PAS, but both optimal and realized growth were invariant to MSP (linear model $p > 0.05$) and did not differ significantly across the MSP gradient (Fig. 3b). Differences between optimal and realized growth were greatest in warmer and drier regions, and no difference was found under cooler, wetter conditions. *Pinus ponderosa* realized growth was reduced by an average of 21 % from optimal growth, a lower average reduction than in either *Pinus contorta* or *Pseudotsuga menziesii*.

Pseudotsuga menziesii realized growth was also invariant across an MSP gradient (linear model $p > 0.05$), yet optimal growth declined significantly with increasing MSP.

Table 2 Parameter values for the selected model for each species, showing both posterior mean values and 95 % credible interval (CI) boundaries

	<i>Pinus contorta</i>	<i>Pinus ponderosa</i>	<i>Pseudotsuga menziesii</i>
β_1			
Mean	0.726	0.676	0.510
2.5 % CI	0.504	0.391	0.330
97.5 % CI	0.964	1.118	0.804
β_2			
Mean	-0.058	-0.046	-0.033
2.5 % CI	-0.168	-0.144	-0.122
97.5 % CI	-0.001	-0.001	-0.001
β_3			
Mean	1.013	0.978	1.039
2.5 % CI	0.856	0.793	0.840
97.5 % CI	1.231	1.225	1.256
β_4			
Mean	1.218	1.681	0.442
2.5 % CI	0.640	0.134	0.036
97.5 % CI	2.262	6.291	1.055
α			
Mean	0.055	0.087	0.084
2.5 % CI	-1.401	-1.914	-1.138
97.5 % CI	1.735	2.404	1.717
ε			
Mean	0.343	0.368	0.257
2.5 % CI	0.218	0.227	0.165
97.5 % CI	0.524	0.576	0.385
τ			
Mean	0.798	1.517	0.551
2.5 % CI	0.223	0.405	0.074
97.5 % CI	1.962	4.449	1.847

β_1 represents the temperature effect, β_2 the precipitation effect, β_3 adjusts the intercept of the logistic crowding relationship, β_4 represents the strength of the crowding effect, α is a random effect for transect that accounts for unexplained abiotic dependence among trees within the same transect, τ characterizes the variance in the random effect, and ε represents the overall model error

Differences between *Pseudotsuga menziesii* optimal and realized growth were greatest in warmer, drier regions, with no difference in cooler, wetter regions. On average, *Pseudotsuga menziesii* realized growth was reduced by 39 % from optimal growth (Fig. 3c).

Discussion

The primary aim of this study was to quantify the relative influences of climate and competition on tree radial growth along montane ecotones. By constructing species-specific

Bayesian models for tree radial growth, we were able to partition the effects of temperature, precipitation, and crowding. Our results show a greater relative influence of climate effects than crowding effects on radial growth, and relatively low competition importance at distribution edges within closed-canopy forests. In the context of climate change, these findings suggest that climate plays an important role in regulating tree growth at local distribution edges, and is likely to be a strong determinant of future distribution dynamics of these montane trees. However, the effects of crowding were also significant, indicating that crowding may mediate tree responses to future climate along ecotones.

Drivers of growth variation

Our findings show generally low competition importance across the range of climate conditions over which we sampled (Fig. 2) along with lower sensitivity of growth to variation in crowding effects than to variation in climate effects (Table 3). Together, these findings indicate that climate is a stronger driver of growth variation than crowding at these distribution edges and that trees at distribution edges may exhibit highly variable responses to climate. These findings suggest that the drivers of growth variation within closed-canopy distribution edges in our study region differ from those across distribution interiors. Studies conducted across distribution interiors have consistently found a greater impact of competition than climate on tree growth (e.g., Clark et al. 2011; Gómez-Aparicio et al. 2011). Within closed-canopy forest interiors, high productivity and strong local abiotic effects generally override the effects of climate (Holman and Peterson 2006). While few other studies have evaluated growth responses at closed-canopy distribution edges, Ettinger et al. (2011, 2013) quantified relationships between climate, tree growth and crowding across the altitudinal ranges of a suite of conifer species in the Pacific Northwest, capturing treeline, closed-canopy distribution edges and distribution interiors. The authors found strong relationships between growth, snowpack and temperature only at the upper range limits of the high-est elevation species. Conversely, relationships between crowding and growth were found to be significant across species altitudinal ranges. These findings were interpreted as suggesting that climate regulates growth at upper limits of physiological tolerance, but within closed-canopy forests (i.e., interior populations and lower distributional limits), crowding drives growth variation. Our contrasting results may be due to the lower productivity and harsher climate in our study region, which may reduce resource competition while simultaneously increasing climatic stress relative to more temperate forests. Additionally, the this study show relatively narrow temperature

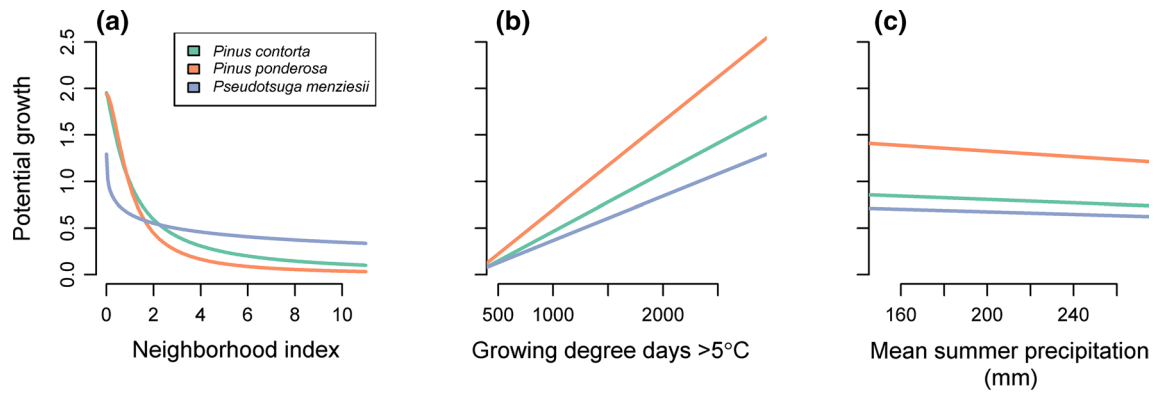


Fig. 1 Individual effects of crowding (a), temperature (b) and precipitation (c) on radial growth of *Pinus contorta*, *Pinus ponderosa* and *Pseudotsuga menziesii*. Crowding and precipitation show mean

negative effects on growth, while temperature shows a mean positive effect. Individual effects are calculated by holding all other parameters and variables at their mean values

Table 3 Sensitivity of model output (mean radial growth) to uncertainty in parameters, as estimated by perturbing each parameter within the range of its posterior distribution

	<i>Pinus contorta</i>	<i>Pinus ponderosa</i>	<i>Pseudotsuga menziesii</i>
β_1	1.741	2.681	1.815
β_2	3.857	7.587	5.755
β_3	0.427	0.433	0.110
β_4	0.019	0.108	0.058
α	0.502	0.769	0.633

Model sensitivity is the derivative of the relationship between perturbed parameter values and model output. β_1 and β_2 represent temperature and precipitation effects, respectively, and β_3 and β_4 account for the effect of neighborhood basal area; α is the random effect for transect

envelopes (Bell et al. 2014a, b), indicating that they may easily meet abrupt physiological temperature limitations well below treeline.

Our models predicted growth of all species to increase with growing season temperature and to decline weakly with summer precipitation, which is consistent with strong temperature limitation on growth (Table 2; Fig. 1). Because we did not include an interaction between temperature and precipitation in the model formulation, it is possible that the contribution of each of these variables traded off in the model-fitting process, making it difficult to draw inference from a comparison of the model's greater sensitivity to precipitation than to temperature. Further, the precipitation parameter was estimated with a broad credible interval (Table 2), indicating that the precipitation response is not well constrained by the data. This could either be due to poor data characterization, or it could reflect variable growth responses to precipitation at the observed scale. Variable and unpredictable relationships between growth and precipitation have been commonly identified in these species, with both positive and negative trends identified (Stohlgren and Bachand 1997; Lo et al. 2010; Miyamoto

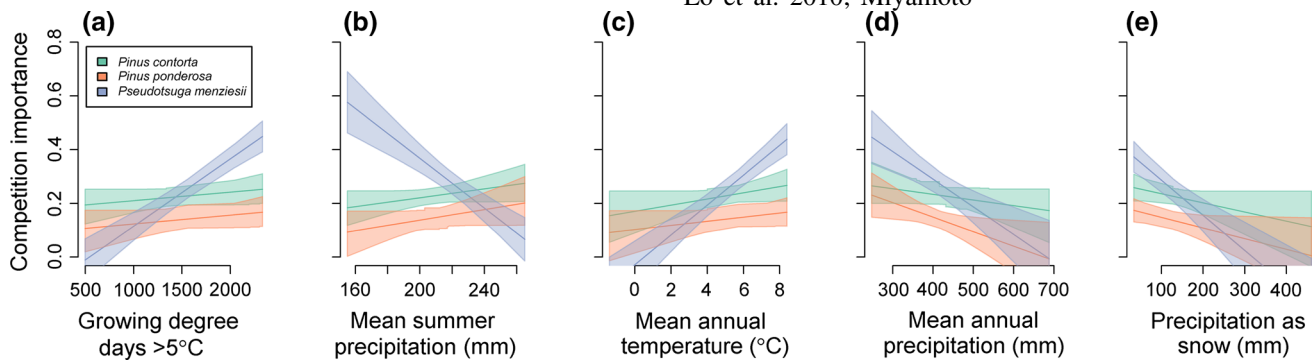


Fig. 2 Competition importance across gradients of growing degree days (a), mean summer precipitation (b), mean annual temperature (c), mean annual precipitation (d) and precipitation as snow (e) was generally the highest and most variable for *Pseudotsuga menziesii*,

while *Pinus contorta* and *Pinus ponderosa* competition importance varied little with climate. Mean competition importance predicted from linear models is presented with 95 % CIs

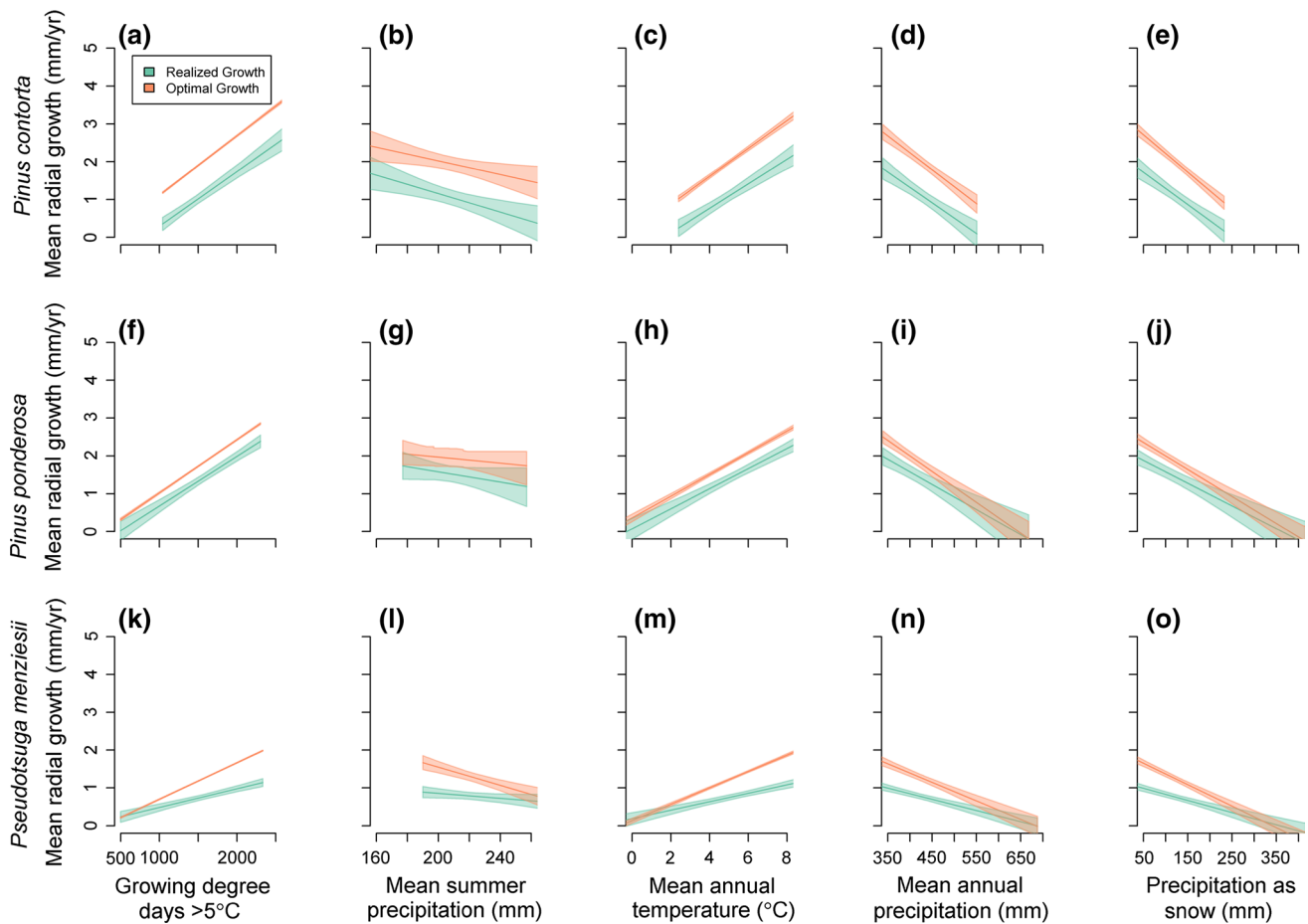


Fig. 3 Modeled realized and predicted optimum growth of *Pinus contorta* (a–e), *Pinus ponderosa* (f–j) and *Pseudotsuga menziesii* (k–o) across climate gradients. In general, optimum growth was higher

et al. 2010). Variation in precipitation-growth relationships is commonly related to the precise timing of precipitation (Chhin et al. 2008; Soulé and Knapp 2011), stand elevation (Lo et al. 2010), edaphic factors (Ogle et al. 2000; Pinto et al. 2007) or crown status (Carnwath et al. 2012), all of which may influence the amount of precipitation that is actually available for uptake by trees. Thus, our 10-year averages of seasonal precipitation and growth trends characterized across a broad geographic range may not provide the temporal or spatial resolution needed to characterize strong directional relationships between precipitation and growth. The strong positive relationship between temperature and growth was better constrained by the data used in our analysis (Table 2) and, consistent with other studies, suggests that temperature may be the most limiting factor for the growth of montane trees (Miyamoto et al. 2010; Klein et al. 2015).

Competition had the greatest effects on growth in warmer and drier regions, where all species showed the highest optimal growth (Figs. 2, 3). Trends of competition

than realized growth, and growth increased towards warm and dry regions. Mean growth and 95 % CIs from linear models are shown

importance for all species were consistent with trends of realized and potential growth across climate gradients; differences between potential and realized growth were greatest where competition importance was highest, demonstrating that crowding has a greater impact on growth in regions of lower climatic stress. A trend of increasing competition importance with decreasing climatic stress has been frequently demonstrated in herbaceous plant communities (e.g., Brooker et al. 2005; Gaucherand et al. 2006), but has been only rarely evaluated in tree communities. In one such study, Kunstler et al. (2011) analyzed competition importance and abiotic stress across gradients of soil water availability and growing degree-days for European montane trees. Similar to our findings, this study found competition importance to be greatest in regions of highest tree growth. In our study, competition importance varied considerably across temperature and precipitation only for *Pseudotsuga menziesii*. This likely reflects greater competition for moisture in drier, productive habitats along with variation in species' physiological moisture stress. Both

Pinus contorta and *Pinus ponderosa* employ stress-avoiding strategies under conditions of moisture stress by adjusting leaf area to sapwood area ratios, thus minimizing the effect of moisture stress on cambium production (Delucia et al. 2000; Carnwath et al. 2012). *Pseudotsuga menziesii*, however, withstands moisture stress by tolerating low water potentials, yet its inability to avoid moisture stress results in dramatic effects on physiological processes, ultimately reducing growth under conditions of moisture stress (Niinemets and Valladares 2006; Carnwath et al. 2012). Consequently, *Pseudotsuga menziesii* growth appears more sensitive to moisture stress, likely resulting from greater competition for moisture in productive, warm habitats, than *Pinus contorta* and *Pinus ponderosa*, which show relatively invariant competition importance across climate gradients.

We recognize that our quantification of competition via crowding is incomplete, as it does not recognize the processes of competition, the influence of potential non-tree competitors, or fine-scale heterogeneity in resource availability. Nevertheless, our neighborhood index does represent the well-documented outcomes of competition in forests, and similar indices have been successfully applied in a multitude of tree competition studies (e.g., Bella 1971; Hegyi 1974; Weigelt and Jolliffe 2003; Canham et al. 2004; Baribault and Kobe 2011; Contreras et al. 2011; Gómez-Aparicio et al. 2011; Kunstler et al. 2011; Aakala et al. 2013). Manipulation of neighborhood basal area via mechanical thinning or deliberate variation in spacing has been shown to result in consistent trends of increased radial growth in these and other species of conifer trees (Barrett 1961; Scott 1998; Wonn and O'Hara 2001; Ferguson et al. 2011; Hood et al. 2012), which can be correlated with changes in soil resource availability following basal area reduction (Gundale et al. 2005). Strong competitive release following stand thinning has been demonstrated for single species stands of *Pinus contorta*, *Pinus ponderosa* and *Pseudotsuga menziesii* in the Northern and Central Rockies (Scott 1998; Ferguson et al. 2011; Hood et al. 2012), although ecotonal stands, which typically occur on steep and inaccessible slopes, have rarely received such experimental treatments (Scott 1998). Thus, while our study does not directly measure resource availability, uptake, or use, the clear relationship identified between neighborhood basal area and tree growth, corroborated by thinning studies demonstrating increased resource availability and competitive growth release, reasonably suggest that changes in neighborhood basal area may influence focal tree growth via competitive mechanisms. Further, within these closed-canopy, dry forests, competition from non-tree vegetation is unlikely to affect growth rates of mature trees (LeMay et al. 2009). Nevertheless, fine-scale resource heterogeneity may interact with radial growth at spatial and temporal resolutions not captured by our 10-year average growth trends

and broad sampling gradients. Thus, competition may exert substantial finer-scale effects on tree growth that cannot be addressed by our approach, and our findings are best interpreted as representing the effects of crowding and climate.

Climate change implications

Climate is changing rapidly in the Rocky Mountain region and is predicted to drastically influence distributions of species (Luckman and Kavanagh 2000; Dobrowski et al. 2013; Bell et al. 2014a, b). Warming temperatures are predicted to drive upslope range shifts of tree species, with significant habitat loss for high-elevation species and increased dominance of lower-elevation species such as *Pinus ponderosa* (Bell et al. 2014a, b). The importance of competition in regulating distribution shifts has been postulated for tree communities (Case et al. 2005; Lenoir et al. 2010; Meier et al. 2010), and has been demonstrated to be an important determinant of performance at distribution edges among other temperate conifer tree species (Ettinger et al. 2011; Ettinger and HilleRisLambers 2013). Our findings demonstrate that climate is the dominant factor controlling growth at ecotonal distribution edges of *Pinus contorta*, *Pinus ponderosa* and *Pseudotsuga menziesii*, with the importance of competition appearing to increase towards regions of lower climatic stress. While distribution shifts will be directly dependent upon establishment and mortality events (Pulliam 2000; Schurr et al. 2012; Bell et al. 2014a, b; Normand et al. 2014), growth is highly correlated with these demographic processes, is easier to observe, and responds more immediately to environmental changes (Kobe et al. 1995; van Mantgem et al. 2003; Wyckoff and Clark 2005; McMahon et al. 2010; Clark et al. 2011; Renwick and Rocca 2015), thus acting as a useful proxy for population sensitivity to climate change. This suggests that climate may be a strong driver of shifts in distribution edges of montane trees. Overall, our results strengthen the findings of studies that have predicted distribution shifts in Rocky Mountain forests by assuming strong associations between climate and habitat suitability (Bartlein et al. 1997; Rehfeldt et al. 2006; Bell et al. 2014a, b). However, our results also demonstrate that competition does contribute measurably, albeit less than climate, to radial growth variation, and we thus caution against complete dismissal of the influences of crowding/competition.

The methods employed in this study make use of a relatively novel approach to reveal the drivers of growth variation along montane ecotones. Our Bayesian modeling approach and sensitivity analysis allow us to more precisely quantify the relative contributions of crowding and climate to growth variation and our data focus specifically within closed-canopy ecotones, allowing us to assess growth responses among populations that are particularly important in the context of distribution shifts, yet have

received little attention. Overall, our findings indicate that climate is the dominant driver of variation in tree growth at closed-canopy distribution edges.

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Authors contribution statement P.E.C.P. conceived and designed the study. P.E.C.P. and E. C. collected field data. E. C. completed tree core analysis and P.E.C.P. conducted all statistical analysis. P.E.C.P. and E. C. wrote the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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