LETTER

Local range boundaries vs. large-scale trade-offs: climatic and competitive constraints on tree growth

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Abstract

Species often respond to human-caused climate change by shifting where they occur on the landscape. To anticipate these shifts, we need to understand the forces that determine where species currently occur. We tested whether a long-hypothesised trade-off between climate and competitive constraints explains where tree species grow on mountain slopes. Using tree rings, we reconstructed growth sensitivity to climate and competition in range centre and range margin tree populations in three climatically distinct regions. We found that climate often constrains growth at environmentally harsh elevational range boundaries, and that climatic and competitive constraints trade-off at large spatial scales. However, there was less evidence that competition consistently constrained growth at benign elevational range boundaries; thus, local-scale climate-competition trade-offs were infrequent. Our work underscores the difficulty of predicting local-scale range dynamics, but suggests that the constraints on tree performance at a large-scale (e.g. latitudinal) may be predicted from ecological theory.

Keywords

Elevation ranges, range constraint mechanisms, range margins, species distributions, stress trade-off hypothesis, tree rings.

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INTRODUCTION

Species geographical ranges have fascinated ecologists for over two centuries as the spatial manifestation of the ecological niche (Humboldt & Bonpland 1805; MacArthur 1972; Colwell & Rangel 2009; Gaston 2009a; Sexton *et al.* 2009). Current unprecedented rates of anthropogenic climate change (Quintero & Wiens 2013) have elevated the need to understand geographical ranges from theoretical importance for ecologists to practical importance for land managers. Broad concordance between species ranges and climate isoclines (Woodward & Williams 1987; Root 1988), palaeo-range shifts during the Quaternary (Williams *et al.* 2004; Jackson & Blois 2015), and ongoing range shifts coinciding with recent anthropogenic warming (Root *et al.* 2003; Lenoir *et al.* 2008; Tingley *et al.* 2012) suggests that climate plays a large role in constraining species ranges. However, recent range shifts are variable, ranging from unexpectedly large shifts to no shifts to shifts in the opposite of the predicted direction, indicating that climate is not the sole driver of range limits (Lenoir *et al.* 2010). Moreover, species interactions are known to complicate the relationship between climate and species ranges (Araújo & Luoto 2007; Ettinger & HilleRisLambers 2013; HilleRisLambers *et al.* 2013). Unfortunately, few useful generalisations about the role of climate vs. species interactions in constraining species ranges have emerged (Gaston 2009b; Angert *et al.* 2011; Buckley & Kingsolver 2012; Sunday *et al.* 2012).

A long-standing ecological hypothesis, the stress trade-off hypothesis [i.e. STH, also the 'Species Interactions-Abiotic Stress Hypothesis' of Louthan *et al.* 2015)] could provide a general framework for predicting geographical range constraints. The STH posits that biotic interactions constrain organismal fitness in benign environments, whereas abiotic stress constrains fitness in harsh environments. The STH underpins famous classical work in many systems (Dobzhansky 1950; Connell 1961; MacArthur 1972; Brown 1995), arguably dating back to Darwin (Louthan *et al.* 2015). Applied to species distributions, the STH implies that species distributed across a climate gradient (e.g. elevation, latitude) should be constrained by species interactions (e.g. competition) at their benign range boundary and by climatic stress (e.g. limits to physiological tolerance) at their harsh boundary (Connell 1961; Loehle 1998; Koehler *et al.* 2012; Savage & Cavender-Bares 2013; Louthan *et al.* 2018). Thus, the STH provides testable predictions about where climate or biotic interactions constrain a species range, and could therefore provide critical guidance for scientists predicting range dynamics for poorly studied species.

A robust test of the STH requires measurements of both climatic and biotic/competitive constraints on organismal fitness across multiple geographical ranges. Unfortunately, few studies examine both climatic and biotic interactions across entire species distributions (Louthan *et al.* 2015, 2018). For example an early study hypothesising that the STH drives North American tree species distributions is based on a qualitative

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synthesis of forestry growth trials (Loehle 1998). Similarly, a burgeoning tree ring literature has documented increased growth sensitivity to climate near high latitude or elevation boundaries (Case & Peterson 2007; Ettinger *et al.* 2011; Griesbauer *et al.* 2011; Lévesque *et al.* 2014; D'Orangeville *et al.* 2016), but since most do not evaluate biotic constraints, they cannot be used to test the STH. A number of tree ring studies have quantified both climatic and competitive constraints, but typically are not designed to detect range constraints (e.g. Martin-Benito *et al.* 2011; Carnwath & Nelson 2016, but see Buechling *et al.* 2017). A few studies do show increasing competitive constraints at low elevation or wet range boundaries (Callaway 1998; Coomes & Allen 2007; Copenhaver-Parry & Cannon 2016; Louthan *et al.* 2018 but see Barton 1993; Ettinger & HilleRisLambers 2013; Sanchez-Salguero *et al.* 2015). However, these studies cover a small number of species, sites, climates and range margins and rarely study both climatic and competitive constraints. Moreover, the STH has received mixed support from small-scale investigations of tree elevation range boundaries (Barton 1993; Ettinger *et al.* 2011; Ettinger & HilleRisLambers 2013) and glasshouse experiments (Koehler *et al.* 2012; Savage & Cavender-Bares 2013). To our knowledge, no study has tested the predictions of the STH in multiple species at a large geographical scale using observations of range constraint mechanisms.

To address these issues, we conducted a multi-species, multi-site analysis of both climatic and competitive constraints on tree growth across the elevation ranges of tree species across a variety of climates in the western USA (Fig. 1). We collected tree cores along three mountains in Colorado (CO), Montana (MT) and Washington (WA), encompassing 17 species' elevation range boundaries (Fig. S1). We focused on three dominant tree species per mountain transect, collecting cores at range centres and high- and low-range margins. The three transects span large climate gradients and cover much of temperate climate space containing forest biomes (Fig. 1c, S2). We used tree rings to reconstruct growth and quantify metrics (see Table 1) of tree growth sensitivity to climate and local competitive environment, typically considered the dominant biotic constraints for trees. We also quantified survival and regeneration. We used tree rings to test the STH by looking for trade-offs between climatic and competitive constraints across altitudinal distributions of focal species (i.e. greater climatic sensitivity at harsh range boundaries, greater effects of competition at benign range boundaries). We also used survival and regeneration data to test for demographic compensation (where growth is inversely correlated with other vital rates, e.g. Doak & Morris 2010; Villellas *et al.* 2015), to formulate hypotheses about range boundaries unexplained by growth constraints. We then examined climate and growth constraints across all species and sites, to test whether the STH emerges as a large-scale trade-off between climatic and competitive growth constraints.

METHODS

Study locations and sampling design

We collected tree cores from 644 trees along three elevation transects, one on Shark's Tooth in the San Juan National Forest, Colorado (henceforth 'CO'); Mt. Brown in Glacier National Park, Montana ('MT') and Hurricane Hill in Olympic National Park, Washington ('WA') (Fig. 1a, Fig. S1). Transects were principally defined by decreasing summer aridity and growing season temperature with increasing elevation (Fig. S2a). The three transects differed considerably in winter/dormant season precipitation (Nov-April), and seasonal temperature variation (continentality) (Fig. S2b).

We identified transects from each mountain base (or in Colorado the lower elevation forest boundary) to the high elevation tree line roughly along a western aspect. We identified the range boundaries of the dominant low elevation, montane and subalpine tree species per mountain by quantifying relative abundances in 3-6 strip transects (5 m wide by 50 m long counting every stem >10 cm DBH) for every *c.* 50 m of elevation gain. Study species (from low to high elevation) are *Pinus ponderosa, Populus tremuloides* and *Abies lasiocarpa* in CO, and *Tsuga heterophylla, Psuedotsuga menziesii* and *Abies lasiocarpa* in MT and WA (Fig. S1). We refer to each species on each transect as a 'species-replicate', as some species were sampled on multiple transects. For each species-replicate, we cored 20-30 trees from each of three populations: the high and low elevation range margins and range centre (Fig. 1b, population and soil summaries in Tables S1 & S2). In total, we examined nine species-replicates, 26 populations (*T. heterophylla* in WA extends to sea level so this species-replicate has no lower range margin), and 17 elevation range boundaries (two per species-replicate except *T. heterophylla* in WA). We determined the mean climate for each population based on the 1961–1990 PRISM climate normals (Daly *et al.* 2008) using ClimateWNA interpolation [ClimateWNA version 5.21, (Wang *et al.* 2012)].

We cored dispersed trees in a *c.* 100 m elevation band in each population, seeking to sample across variation in microtopography and stand history within each population. We cored 10–15 pairs of mature canopy trees (total of 20–30 trees) per population, including a range of diameters representative of the forest structure. Trees in a pair were < 30 m apart and of similar diameter, one growing in a high competitive environment and one in a low competitive environment (typically a 10 + year-old tree-fall gap). Pairs of trees were > 40 m apart and located away from visible drainages, and we avoided trees with obvious recent changes in competitive environment. We quantified competitive environment using multiple metrics: stand basal area (from a variable radius wedge prism), number of canopies touching the focal tree, the focal tree's active crown fraction (percent of total tree height supporting foliage, measured with an inclinometer and digital range finder) and number of trees within 5 m of the focal tree. These metrics captured the majority of growth variation found in size- and distance-weighted competition metrics in the CO transect (Anderegg & HilleRisLambers 2015), yet could be rapidly measured. We counted recent dead conspecific trees [those retaining needles or all bark and fine twigs, assumed to have died within about 5 years (Hicke *et al.* 2012)] in the wedge prism plot around each tree to estimate survival rates. Finally, we counted all conspecific saplings and seedlings within 5 m of the focal tree with a height > 5 cm but a DBH < 5 cm to estimate regeneration.
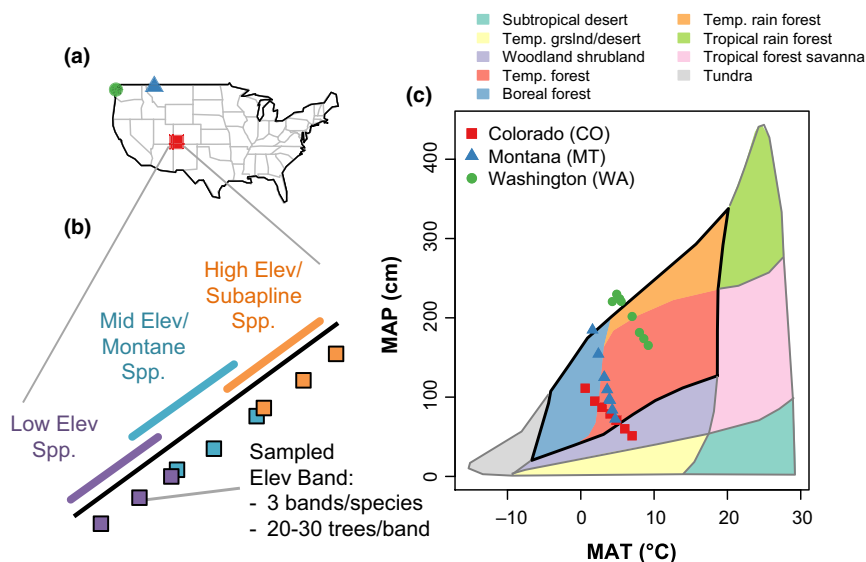
Figure 1 Overview of sampling design. (a) Three sampled mountain transects in the western USA. (b) Sampling scheme across the elevation range of one low elevation, montane and subalpine species per transect. (c) Transects in Mean Annual Temperature (MAT) – Mean Annual Precipitation (MAP) space based on 30 year climate normals from (Wang *et al.* 2012), plotted over Whittaker's biome map (Whittaker 1975) – the transects cover much of temperate forest biome climate space (outlined in black).

Table 1 Explanation and justification of metrics used to test the Stress Trade-off Hypothesis using tree rings.

	Environmental harshness	Competitive constraint	Climatic constraint
Metric	Mean growth rate	Growth sensitivity to competition	Population growth synchrony
Details	Size- and competition-standardised mean Basal Area Increment from 2003 to 2012, calculated using linear mixed effects models	Suppression of mean Basal Area Increment from a standardised increase in neighbourhood density (based on tree-to-tree variation in mean growth)	Mean correlation of annual growth anomalies between trees in a population (synchrony of growth through time)
Rationale	Mean growth rates (at mean competitive density) will reflect general environmental harshness, with slower growth rates indicating a harsher environment	Large growth differences between trees growing in low and high neighbourhood densities indicate that competition greatly constrains tree growth	Synchronous growth between widespread trees indicates a broad-scale driver (i.e. climate), whereas asynchronous growth indicates that local factors (competition, pests) drive growth anomalies

We collected two tree cores at 1.35 m height from opposite sides of each tree perpendicular to the aspect. Cores were mounted on blocks, sanded and scanned at high resolution, and annual growth rings were measured to 0.001 mm using

WinDENDRO (Version 2008e; Regent Instruments, Quebec City, Quebec, Canada). Cores were visually crossdated in WinDENDRO and then statistically crossdated in R with the *dplR* package [version 1.6.4, (Bunn 2010), see Table S3 for full crossdating details, all final chronologies had an Expressed Population Signal > 0.87]. One tree could not be crossdated and was excluded. Ring widths from the two cores per individual were then averaged.

Mean growth and competition

Ring width data were analysed in two ways. First, to assess the effects of competitive environment and range position on mean growth (columns 1 & 2 in Table 1), we used annual ring widths, tree diameter, and bark depth to calculate Basal Area Increment (BAI) from the outside of the tree inward for each tree. We then calculated mean annual BAI for each tree for 2003–2012, when competitive environment metrics assessed in 2013 were likely accurate. We estimated size- and competition-standardised mean growth (our metric of environmental harshness) for each population from linear mixed models for each species-replicate relating mean BAI to range position and some combination of tree size and competitive environment. Specifically, we determined the best random effect structure for each species-replicate (Zuur *et al.* 2009) and then built models relating mean BAI to all combinations of population, tree DBH, one or two non-colinear competitive metrics, population-by-DBH, population-by-competition and DBH-by-competition interactions and multiple variance structures. We then selected the best model for each variance structure based on AIC and selected the most parsimonious model from these best models based on AIC (see Supplemental Methods: Mean Growth and Growth Sensitivity to Competition). Possible competitive metrics included up to two of: stand basal area,

tree active crown fraction, number of touching crowns and number of trees within 5 m. Significant differences in mean growth between range margins and the range centre at the mean size and competitive environment for each species-replicate were determined by centring predictors on species-replicate means and comparing range margin intercepts to the range centre intercept with *t*-tests. We interpret size- and competition- standardised mean growth as an indication of the environmental suitability, with low growth interpreted as environmentally 'harsh' and high growth as environmentally 'benign'. We used pairwise contrasts based on *t*-tests to assess the statistical significance of the range margin sensitivities to competition compared to the range centre (e.g. significance of the population-by-competition interactions). To visually compare populations, the effect of competition on growth is represented as the raw growth suppression for each population resulting from a species-replicate one standard deviation increase in competitive environment, holding DBH constant at the species-replicate mean. See Table S4 for the final model used for each species-replicate.

Climatic growth constraints

Second, we used tree ring widths to estimate growth synchrony between trees in a population, as a metric of climatic growth constraints. We created unitless ring width index (RWI) time series by detrending each tree's ring width chronology using a spline (Bunn 2010) and then pre-whitening with an AR1 autoregressive model. Synchronous growth fluctuations across all trees in a population suggest that broad-scale factors, likely climate, drive growth fluctuations. Conversely, asynchronous growth suggests that local factors (pathogen attack, mechanical damage, changes in competitive environment) drive growth fluctuations for individual trees (Ettinger *et al.* 2011; Shimatani & Kubota 2011; Shestakova *et al.* 2016). Other broad-scale factors that may influence all trees in a population, such as soil parent material and nutrient availability, should influence mean growth without *synchronising* growth year to year across trees. Thus, growth synchrony is a simple and intuitive proxy for climate constraint that is agnostic to the climate variables actually constraining growth. Competitive interactions between long-lived trees are likely to remain relatively stable over multiple years, even if monotonically increasing over time, thus making our metrics of climatic and competitive sensitivity independent rather than mutually exclusive. We quantified growth synchrony using the distribution of pairwise correlations (Pearson's *r*) between the RWI of all trees in a population (trimmed to the shortest time-series for each species-replicate, Table S3). We assessed significant synchrony differences between range margins and the range centre using beta-regressions (correlation coefficients were transformed to be bounded 0–1) with a logit link, elevationally varying precision and pairwise contrasts with the range centre.

We originally assessed climate sensitivity with models relating tree growth to several climate variables, but found growth synchrony to be the most parsimonious, assumption free and easily interpretable metric. In brief, we fit linear mixed-effects models which predicted RWI as a function of one or several climate variables (see 'Climate Data' section of Supplementary

Methods), exploring multiple metrics of climate sensitivity such as the size of standardised climate coefficients, ΔAIC of best model from null model, marginal or conditional R^2 of best model, etc. However, inferences proved highly dependent on which of many climate data sets, model selection techniques and methods for selecting potential climate covariates were employed. Results from these analyses qualitatively agreed with the growth synchrony results presented here, and we therefore chose to focus on growth synchrony as an index of climate sensitivity. See Supplemental Methods: Alternative Metrics of Climate Sensitivity for these methods and results, and the difficulties we faced applying these approaches.

Recruitment and survival

Survival probabilities were calculated for each population based on the proportion of live vs. recent dead (died within the last *c*. 5 years) conspecific trees measured in the wedge prism basal area plots around each cored tree. We turned count data of living and recently dead trees into binary survival data, applying generalised linear mixed models with a binomial error distribution, a logit link function and a random plot effect to model recent survival as a function of range position (see Table S5 for full details).

To estimate recruitment, we modelled sapling and seedling density for each species-replicate as a function of population, competitive density (either total stand basal area, stand basal area of conspecifics, or number of stems >10 cm DBH within 5 m) using generalised linear models with a Poisson distribution and log link. Model structure (and best competitive environment predictor) was selected based on model AIC (see Table S6 and Fig. S6), and used to predict regeneration densities for each population at species-replicate mean competitive densities. Recruitment of *Pinus ponderosa* in Colorado could not be modelled in this way because sapling/seedling densities were extremely low. Instead, we present the median sapling/seedling densities from 10 additional 10 × 50 m seedling transects. We tested for consistent relationships between adult growth and both recruitment and adult survival across all species-replicates using linear mixed-effects models with mean growth as a fixed effect and species-replicate as random slopes and intercepts.

Broad-scale test of STH

Broad-scale relationships between mean growth and growth synchrony/sensitivity to competition were assessed across all species-replicates using hierarchical linear mixed effects models, with mean growth as a fixed effect and species-replicate as random slope and random intercept effects. Models were constructed with both unweighted and inverse standard error-weighted data. Results were qualitatively similar so only SE-weighted *P*-values are presented. Reported *P*-values are *t*-tests for the significance of the fixed effect of mean growth based on Satterthwaite's estimated degrees of freedom.

Statistical models were fit in the R statistical environment (version 3.2.4, R Core Team 2016), using functions in the *stats, nlme, lme4, lmerTest* and *betareg* R packages (Cribari-Neto & Zeileis 2010; Bates *et al.* 2015; Kuznetsova *et al.* 2016; Pinheiro *et al.* 2016). Code can be found in

Supplemental Materials: Example Code. Example Data Sets for Example Code are available as SI Data S1–S3, and full data can be found in the Dryad repository associated with this paper (Anderegg & HilleRisLambers 2019, https://doi.org/10.5061/dryad.k5k9074).

RESULTS

STH and local elevation range boundaries

We found a few cases supporting the trade-off predicted by the STH, that species performance is climatically constrained at harsh boundaries but competitively constrained at benign boundaries (Fig. 2). For example *Pinus ponderosa* in Colorado showed a large increase in basal area growth moving from the low elevation (hot-dry) range margin to the high elevation (cool-wet) range margin, suggesting that low elevations are more environmentally harsh and high elevations benign (Fig. 2b). Climatic growth constraints (i.e. growth synchrony) increased from the high-range margin to the low margin ($P < 0.0001$ for high to centre, and centre to low comparisons, Fig. 2f, Table S4), consistent with a climatically controlled lower range boundary and decreasing climatic constraints with elevation. Meanwhile, the strength of competitive suppression was small at mid and low elevation, but became much larger at the high elevation margin (Fig. 2j, linear mixed effects model $P = 0.0041$), consistent with an increased competitive constraint at *P. ponderosa*'s high elevation, benign boundary.

However, most other species did not show evidence of a trade-off between climatic and competitive range constraints (Fig. 2d, h, l, and m). For example growth of *Pseudotsuga*

menziesii from Washington changed little from low to high elevations, suggesting only a slight environmental harshness gradient (Fig. 2c, Table S4). Contrary to expectations, growth synchrony peaked at this species-replicate's range centre (Fig. 2g), and growth sensitivity to competition did not differ significantly across elevation (Fig. 2k, Table S4). In the end, a climate-competition trade-off in adult growth emerged for only two of nine species-replicates (Fig. 2m).

Despite the limited support for the STH at local elevation boundaries, useful patterns for understanding climate change induced range shifts did emerge. All but one species-replicate reached its maximum growth rate at one range boundary and minimum growth rate at the other (Fig. 2d, Fig. S3, Table S4). Thus, even though some species (e.g. *P. tremuloides* in CO) likely spanned confounding cold and drought stress gradients, most species-replicates appeared to have one 'harsh' and one 'benign' range boundary. Importantly, seven of nine of these species showed evidence of climatic growth limitation at these harsh range boundaries (Fig. 2m). However, only three of eight species-replicates showed evidence of competitive constraints at benign range boundaries (one species-replicate had only one range boundary, see Methods).
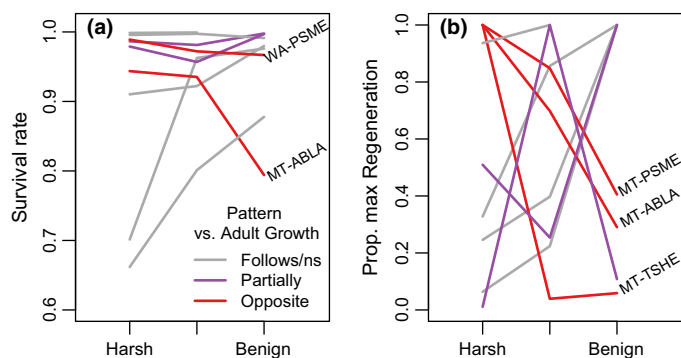
Our results also highlight the difficulties of identifying the 'harsh' range boundaries likely to be most sensitive to climate change. Our growth-rate-related metric of environmental suitability identified both harsh upper margins (4/9 species-replicates) and harsh lower range margins (5/9 species-replicates), defying simple links between harshness and elevation sometimes posited in the literature (e.g. studies reviewed in Louthan *et al.* 2015). In fact, the location (upper vs. lower) of harsh range margins was not consistent for the same species
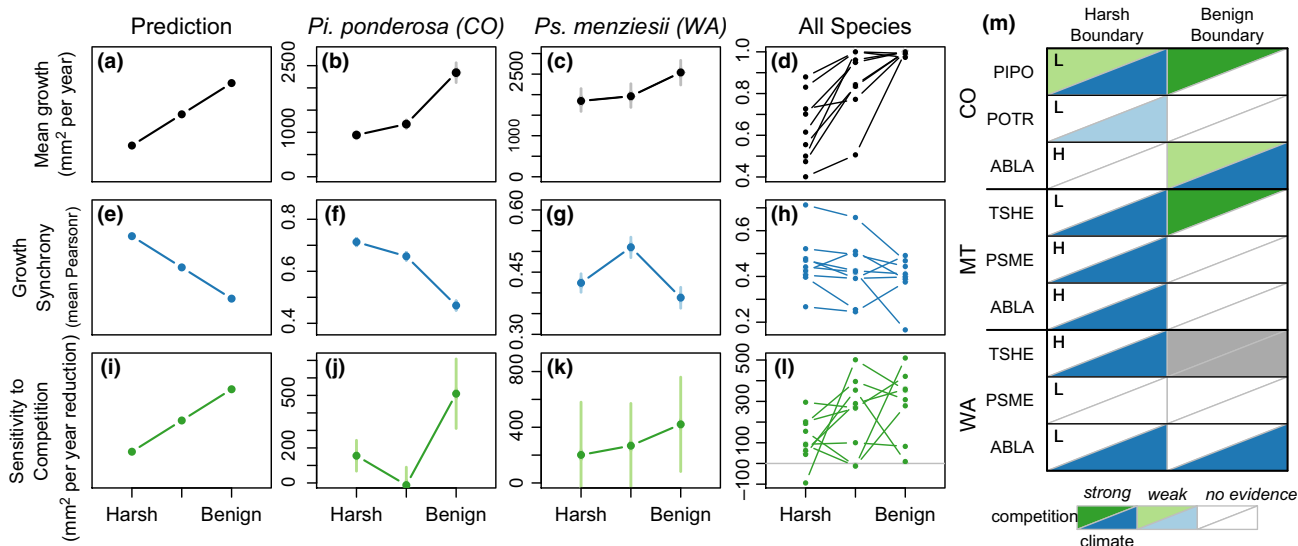
Figure 2 Predicted (a, e and i) and observed (b–d, f–h, j–l) patterns of mean basal area growth (a–d), growth synchrony (e–h), and growth sensitivity to competition (i–l). Error bars show ±SE. Note, the y axis for panel d is proportion of species-replicate maximum growth, rather than mm²/year as in (a–c). Evidence for climatic and competitive constraints for 17 tree elevation range margins is summarised in (m) (see also Table S4). The STH predicts a climatic constrain (blue) at harsh boundaries and a competitive constraint (green) at benign boundaries. Letter in the Harsh column indicates whether the harsh boundary was low ('L') or high ('H') elevation. Gray cell for *T. heterophylla* in Washington was not sampled. Strong evidence: $P < 0.01$ difference between range margin and range centre, weak evidence: $0.1 > P > 0.01$ (or that competitive constraint was much stronger at the other range margin for *Pi. Ponderosa* in CO). PIPO: *Pinus ponderosa*, POTR: *Populus tremuloides*, ABLA: *Abies lasiocarpa*, TSHE: *Tsuga heterophylla*, PSME: *Pseudotsuga menziesii*.

on different transects or for different species on the same mountain (Fig. 2m, Fig. S4). A more nuanced expectation of environmental harshness might predict that harsh range boundaries predominate at the edge of the forest biome (e.g. Fig. 1b). This expectation holds for high and low elevation species in MT and CO (see Fig. S3), where the highest alpine populations and lowest low elevation populations grow most slowly. However, it fails in WA, and provides no useful expectation for the range boundaries of montane/mid elevation species.

We found regeneration and survival were not always correlated with adult growth, potentially indicating demographic compensation. For example two species-replicates had low survival (and high growth) at their benign range boundary and high survival (and low growth) at their harsh boundary (Fig. 3a, Fig. S3, Table S5). In three additional species-replicates, recruitment decreased from the harsh range boundary to the benign boundary, opposite of growth patterns (Fig. 3b). Of these three (all in MT), one species-replicate (*A. lasiocarpa*), showed both a decrease in recruit density and an increase in the sensitivity of recruitment to competitive environment (Table S6). These recruitment patterns generally held true across different seedling/sapling size classes (Fig. S8), and statistical results were quantitatively similar if seedlings and saplings were modelled separately. We also found some evidence for a switch from competition to facilitation in two species-replicates, based on the regeneration sensitivity to overstory competition (Table S6). However, survival and regeneration followed the same elevational patterns as mean growth (i.e. low at the harsh range boundary and high at the benign range boundary) in roughly half of species-replicates (Fig. 3). As a result, there was no significant relationship between survival and mean growth, recruitment and mean growth, or survival and recruitment across all populations from all species-replicates (P-values > 0.1, hierarchical linear mixed effects models, Fig. S9).

Broad-scale evidence of STH

Although the STH did not consistently predict growth constraints at individual range boundaries, we found evidence across all species and sites for the STH at large scales. Specifically, we found evidence for greater climatic growth constraints in harsh environments; populations that grew more slowly on average had more synchronised annual growth (Fig. 4a, inverse SE-weighted linear mixed effects model $P = 0.045$). We also found that the fastest growing populations of trees (in the most benign environments) showed the largest growth suppression due to competition (Fig. 4b, $P = 0.001$). Thus, at a large scale, tree populations in optimal conditions appear to be most constrained by competition, with those in less optimal conditions more constrained by climate. This trend of increasing competitive constraints with increasing growth was qualitatively similar, but not statistically significant, if expressed as a proportion of mean growth rather than raw Basal Area Increment reduction (Fig. S5). A majority of species-replicates showed similar patterns for raw and proportional sensitivity to competition, but a small number of species-replicates with strong growth differences across elevation but minimal differences in sensitivity to competition likely caused proportional sensitivity to be non-significant (see Fig. S6). The relationship between synchrony and sensitivity to competition themselves across all sites was negative but not statistically significant ($0.2 > P > 0.1$, depending on modelling method, data not shown), likely due to the joint uncertainty in both climate and competition sensitivity being larger than the uncertainty in mean growth rate.

Despite this large-scale pattern of increasing climate sensitivity and decreasing sensitivity to competition at harsh sites, there were few clear and intuitive links between tree growth dynamics and macroscale climate. Climatic harshness (i.e. mean growth), growth synchrony and competitive sensitivity did not map onto large-scale climatic gradients (e.g. mean
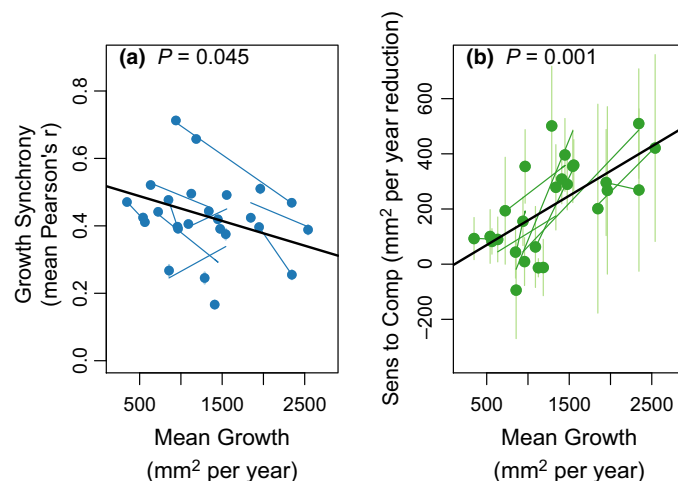

Figure 3 (a) Recent (*c*. 5 year) survival rates and (b) sapling/seedling density (at mean stand density) as a proportion of species-replicate maximum recruitment density vs. range position for nine species-replicates. Red lines show species-replicates that strongly differ from patterns of adult mean growth, purple lines species-replicates that partially diverge from adults, and gray lines species-replicates that follow adult growth or show no significant clinal variation. Labels identify red species-replicates (labels as in Fig 2).

Figure 4 Population growth synchrony (a) and growth sensitivity to competition (b) vs. population mean size- and competition-standardised growth rate across all species-replicates. Points indicate population means, error bars are the standard error of mean parameter estimates, coloured lines show trends for each species-replicate, and the black line shows the global trend line from hierarchical linear mixed effects models. P values indicate the significance of the global trend (inverse SE-weighted).
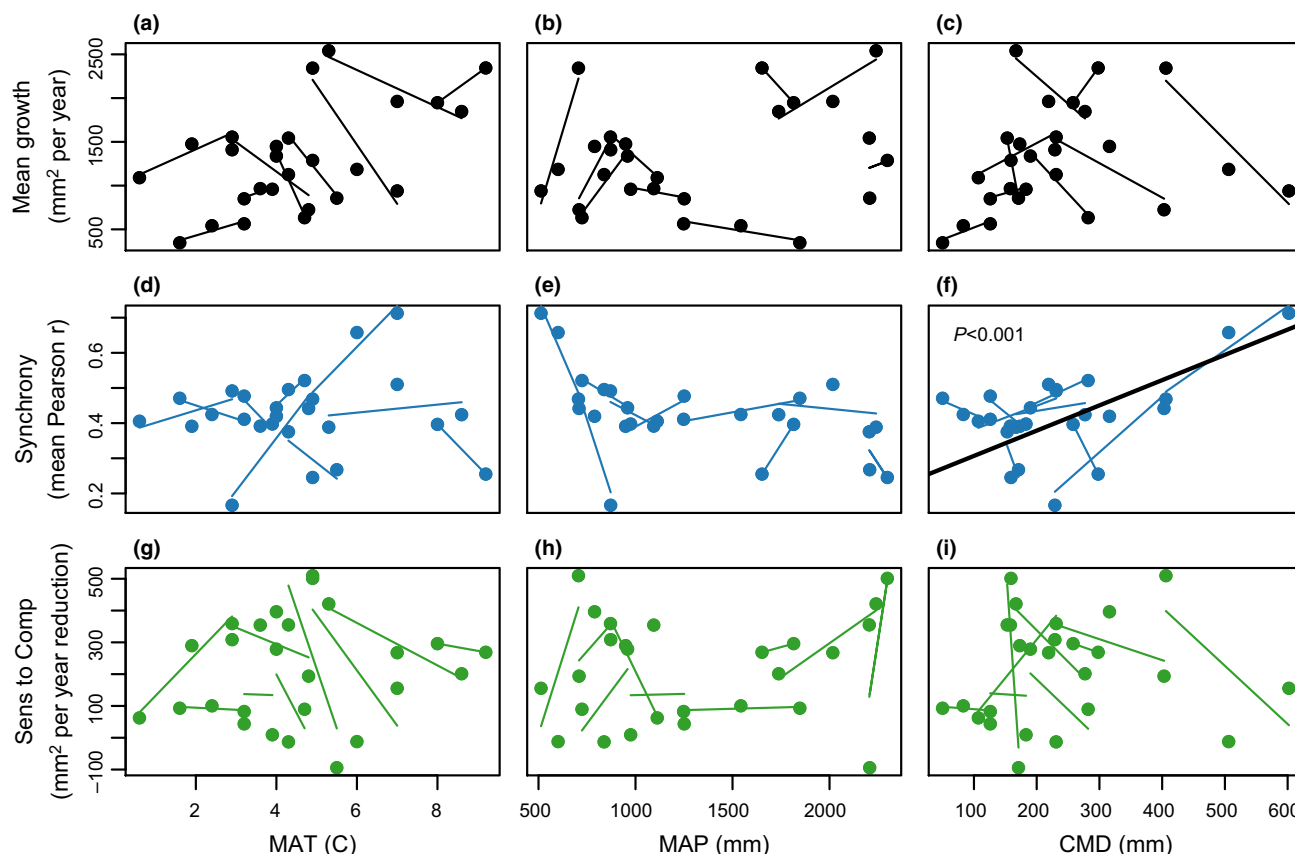
Figure 5 Mean growth (size- and competition-standardised, a–c), growth synchrony (d–f) and sensitivity to competition (g–i) vs. climate. Points, lines and *P*-values as in Fig. 4. MAT: Mean Annual Temperature, MAP: Mean Annual Precipitation, CMD: Climatic Moisture Deficit (Potential Evapotranspiration – MAP).

annual temperature; Fig. 5). Contrasting local responses and regional responses were apparent for some relationships (lines showing within-species-replicate patterns vs. overall trend across all populations, e.g. mean growth and MAT, Fig. 5a), reminiscent of local vs. regional patterns in tree growth in the Eastern U.S. (Canham *et al*. 2018). However, the only significant large-scale relationship was between growth synchrony and CMD, which was driven primarily by the strong response of the driest species-replicates (*P. ponderosa* in Colorado, Fig. 5f).

DISCUSSION

Across our entire data set, competitive constraints generally increased, whereas climatic constraints generally decreased when moving from harsh sites to benign sites (Fig. 4). This provides evidence for the stress trade-off hypothesis at large scales (e.g. across the western USA) and suggests that it may be a useful guiding principle for predicting the range dynamics of large-scale tree distributions. However, we found less evidence that a trade-off between competitive and climatic constraints consistently explains the local elevation ranges of individual species, though climate was typically a dominant constraint at harsh range boundaries (Fig. 2j).

The preponderance of climatic range constraints at harsh boundaries emerged across a wide range of climatic conditions

(Fig. 1), and mirrors single species or single site dendroecological studies (Nakawatase & Peterson 2006; Case & Peterson 2007; Griesbauer *et al*. 2011). Together, this suggests that identifiably harsh range boundaries tend to be under climatic control (but see Urli *et al*. 2016), providing a useful rule of thumb for where correlative distribution models may be used to forecast changes in suitable habitat under climate change.

However, identification of 'harsh' range boundaries at local scales is not always straightforward. Elevation was a poor predictor of harshness (Fig. S4). Proximity to the edge of the forest biome (e.g. *A. lasiocarpa* at high elevation and *P. ponderosa* and *T. heterophylla* low elevation tree lines, Fig. 1) was a better predictor, but also imperfect. Anomalies included *A. lasiocarpa* in WA and CO. In WA, where tree line *A. lasiocarpa* had the fastest radial growth rate of any population, this may indicate a non-equilibrium range boundary or perhaps microclimatic variation that can swamp assumed elevation effects near tree line (Ford *et al*. 2013). Meanwhile *A. lasiocarpa* in CO, which did not show increased climatic constraint at treeline, may experience edaphic constraints (i.e. lack of soil) that control its upper range limit (Fig. 2). Additionally, because mid elevation species did not approach biome boundaries, the direction of their environmental stress gradient could not be predicted based on biogeography alone. This complicates the *a priori* identification of 'harsh' range boundaries, where species are

likely to be climatically constrained and most sensitive to climate change.

We found comparatively fewer instances of competitive than climatic range constraints. This may indicate that competitive range constraints are less prevalent. However, it may also reflect the statistical and biological difficulty of detecting competitive constraints. For one, our competitive metrics were likely imperfect proxies for the actual strength of competition, compared to distance-weighted metrics for example (e.g. Contreras *et al.* 2011). Second, despite selecting focal trees without obvious recent changes to their competitive environment and examining growth from only the most recent decade, current competitive environment may not perfectly reflect the actual competitive environment that affected past growth. Third, a sample size of 20-30 trees per population may be insufficient to confidently detect differences in the strength of competition between populations. Finally, our choice of absolute rather than relative growth suppression to measure sensitivity to competition (see Fig. S6 for justification) requires additional validation. In all, we are thus more confident in our measure of climate sensitivity than competitive constraints, and more confident in our estimation of mean growth than both sensitivities. This may also explain why climatic and competitive sensitivities themselves showed a qualitative but not statistically significant trade-off across our entire data set. Future work is required to overcome these concerns.

In addition, the strongest competitive constraints may primarily affect regeneration rather than adult trees in closed canopy forests (Ettinger & HilleRisLambers 2013). We found suppressed recruitment at the benign range boundary of three species-replicates and evidence in at least one species-replicate (*A. lasiocarpa* in MT) that the negative effect of adult competition on regeneration is highest at the benign range boundary (a boundary unexplained by adult growth sensitivity to competition, Fig. 2m, Fig. 3b, Table S6). Unfortunately, many focal species show episodic recruitment that makes a snapshot of sapling/seedling abundance an imperfect proxy for actual recruitment success. Range constraints acting on establishment and recruitment rather than adults may be quite common (Jackson *et al.* 2009), and should be a major focus of future research.

Moreover, biotic interactions other than competition constrain many benign range boundaries. For example decreased survival (documented in two species-replicates) or recruitment (seen in three species-replicates) at benign range margins may be due to increased pathogen attack. If we assume that all instances of decreased survival or recruitment at benign range boundaries indicate biotic constraints (Fig. 3), the majority of benign range boundaries show some evidence for a biotic limitation (Fig. S10). In this case, two additional species-replicates (*P. menziesii* and *A. lasiocarpa* in MT) show STH trade-offs in growth vs. biotic constraints, increasing support for the STH at local scales.

Finally, the strong effect of large-scale disturbance on some species may also complicate the detection of STH trade-offs at local scales. For example in the mesic, old growth forests of Washington, distributions of *P. menziesii* (requiring high light to regenerate) and *T. heterophylla* (intolerant to fire, but capable of regenerating under low light) may be the legacy of stand replacing fires with multi-century return intervals (Agee

1993) spanning larger spatial extents than we sampled (Wetzel & Fonda 2000). If so, local elevation range margins, particularly in WA, may actually represent the distribution of historic fires rather than a physiological limit for adult trees. Indeed, some species-replicates showed elevational differences in tree size which did not mirror mean growth trends (see *T. heterophylla* in Montana and *P. menziesii* in Washington in Table S1), potentially suggesting that large disturbance events homogenised stand age within populations at landscape scales that our sampling strategy could not capture (Wetzel & Fonda 2000). In this case, even if disturbance (e.g. fire) is a function of climate at larger spatial scales, we might expect noisy local-scale results due to a scale mismatch between mosaic-creating disturbance and local sampling within a single landscape patch.

CONCLUSIONS

Our findings suggest that the stress trade-off hypothesis may be useful for inferring climate change responses at broad spatial scales (e.g. latitudinal range shifts). This is especially true in environmentally 'harsh' regions, where range boundaries are likely to be constrained by climate. One major implication of our work is that high latitude range boundaries or subcontinental dry range boundaries are likely climatically constrained for many trees. Thus, correlative models such as Climate Envelope Models may provide useful predictions of future dynamics of these range boundaries, assuming the dynamics of range contraction or expansion are understood. At the same time, our findings also highlight complexities that complicate the use of correlational tools for forecasts at finer spatial scales (e.g. altitudinal range limits) and at benign range boundaries. However, these complexities are fruitful areas of future study. For example the life-history stages at which population growth is constrained and the importance of competition vs. other biotic interactions as biotic constraints are major unknowns. Landscape-scale disturbance and complex microclimate also serve to increase biogeographical noise at local scales, and understanding the spatial scale at which these factors dominate is important for predicting local-scale range dynamics. Despite these complexities, we are cautiously optimistic that future work will allow for generalisations about range constraint mechanisms that can guide the development and application of range shift modelling tools. We also hope that explicitly biogeographical studies of tree regeneration and survival constraints (paired with studies on tree growth) will improve our understanding of population dynamics at range boundaries, and thereby yield knowledge at the scale relevant for land-management.

AUTHORSHIP

LDLA and JHRL designed the study; LDLA collected the data; LDLA performed the statistical analysis and wrote the first draft of the manuscript, LDLA and JHRL revised the manuscript.

DATA ACCESSIBILITY STATEMENT

Example data and code demonstrating the main analyses are available as Supplemental Information, and full data are available at https://doi.org/10.5061/dryad.k5k9074 in the Dryad repository associated with this paper (Anderegg & HilleRisLambers 2019).

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