

# Recruitment limitation of long-lived conifers: implications for climate change responses

STEVE J. KROISS<sup>1</sup> AND JANNEKE HILLERISLAMBERS

*Biology Department, University of Washington, Seattle, Washington 98195 USA*

**Abstract.** Seed availability and suitable microsites for germination are likely to severely constrain the responses of plant species to climate change, especially at and beyond range edges. For example, range shifts may be slow if seed availability is low at range edges due to low parent-tree abundance or reduced fecundity. Even when seeds are available, climatic and biotic factors may further limit the availability of suitable microsites for recruitment. Unfortunately, the importance of seed and microsite limitation during range shifts remains unknown, since few studies have examined both factors simultaneously, particularly across species' ranges. To address this issue, we assessed seed availability and the factors influencing germination for six conifer species across a large environmental gradient encompassing their elevational ranges. Specifically, we assessed (1) how parent-tree abundance influences annual seed availability; (2) how seed limitation varies across species' ranges; (3) how climatic and biotic factors affect germination; and (4) how seed and suitable microsite availability covary annually within and among species. We found that seed availability declined toward species' upper range edges for most species, primarily due to low parent-tree abundance rather than declining fecundity. Range expansions are thus likely to be lagged with respect to climate change, as long generation times preclude rapid increases in tree density. Negative impacts of canopy cover on germination rates suggest range shifts will further be slowed by competition with existing vegetation. Moreover, years of high seed production were generally correlated among species, but not correlated with the availability of suitable microsites, implying that seedling competition and the interaction between seed and microsite limitation will further constrain recruitment. However, the nature of microsite limitation varied strongly between treeline and low-elevation species due to differing responses to snowpack duration and competition, suggesting that treeline species may be quicker to shift their ranges in response to warming than low-elevation species. In all, our results demonstrate that seed and microsite limitation will likely result in lagged responses to climate change but with differences among species leading to complex range shift dynamics.

**Key words:** *climate change; conifers; elevation gradient; establishment; mast; microclimate; Mount Rainier National Park, Washington, USA; range shifts; regeneration niche; seedlings; species distributions.*

## INTRODUCTION

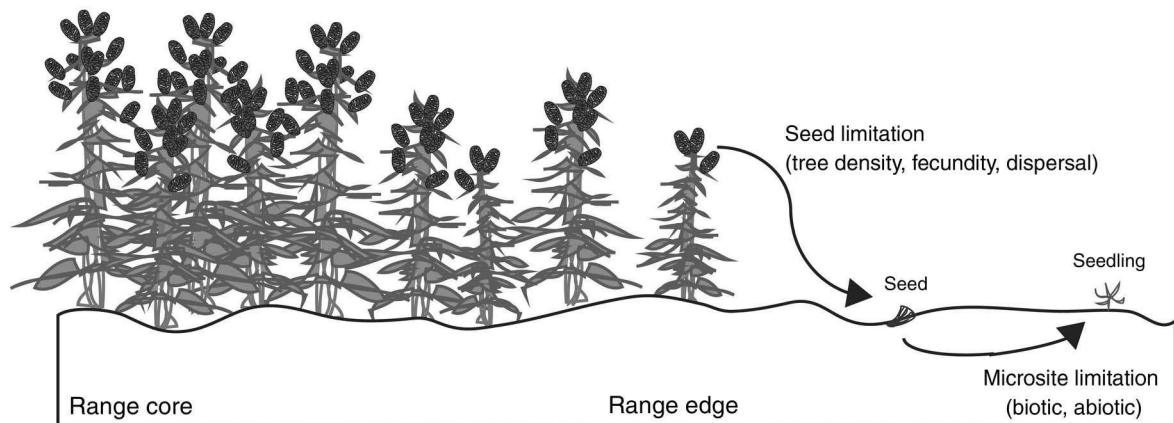
How rapidly tree species shift their ranges in response to climate change will depend on what processes constrain recruitment. This is because sessile trees can only expand their ranges under two conditions: (1) if sufficient numbers of seeds arrive at suitable microsites (Primack and Miao 1992, Ehrlén and Eriksson 2000, Myers and Harms 2009) and (2) if climate change increases the availability of suitable microsites for recruitment (Eriksson and Ehrlén 1992, Nathan and Muller-Landau 2000, Turnbull et al. 2000). Thus, the relative importance of seed and microsite limitation, and the factors governing them, is critical to determining how forests will respond to climate change (Jones and Moral 2009, Dullinger and

Hülber 2011). Furthermore, understanding the nature of seed and microsite limitation may help explain why many plant species have failed to shift their ranges to higher elevations or latitudes despite significant anthropogenic climate change in the last century (Harsch et al. 2009).

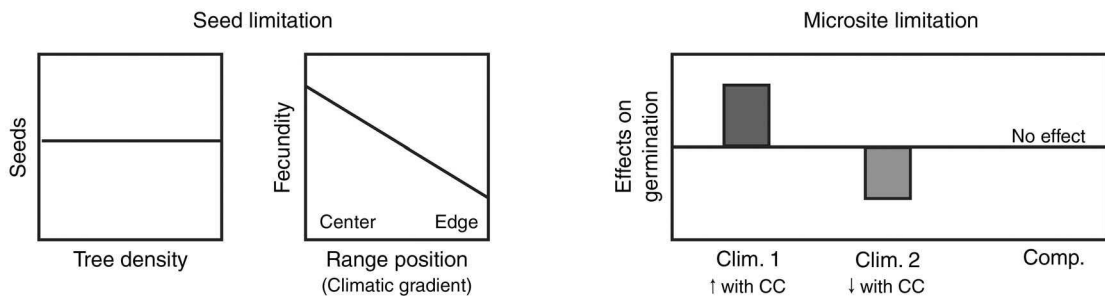
Seed limitation may influence species' abilities to respond to climate change if seed availability is constrained by parent-tree abundance, proximity, or fecundity (Clark 1998, Caspersen and Saprundoff 2005), especially at range edges (Aitken et al. 2008, Sexton et al. 2009). For example, parent-tree abundance can limit seed availability through a combination of fewer seeds being produced and greater distance to seed producing trees (Fig. 1B). If so, then range expansions may be slow since newly establishing individuals at the leading range edge will need to reach reproductive maturity, reproduce, and increase in abundance before further expansion can occur (Platt et al. 1988). Conversely, if seed limitation is primarily due to climatically constrained

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<sup>1</sup> E-mail: skroiss@uw.edu



### A) Range shifts facilitated by recruitment during warming



### B) Range shifts constrained by recruitment limitation during warming

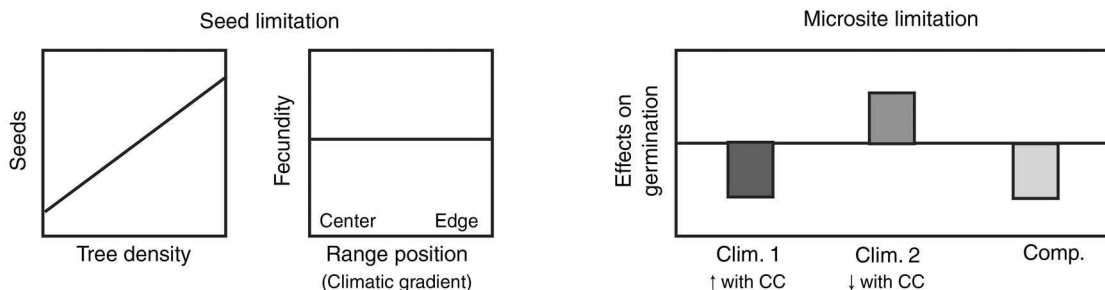


FIG. 1. Potential impacts of recruitment limitation on climate-change-induced range shifts. In panel (A), recruitment facilitates species' responses to climate change (CC) because (1) seed availability is high, even at low abundances (due to high seed production and/or long dispersal distances); (2) fecundity is limited by climatic factors that will become less limiting; (3) germination is limited by climatic factors (clim. 1 and clim. 2) that will become less limiting; and/or (4) germination is not limited by competitive effects from other species (comp.). Conversely, recruitment may constrain species' responses to climate change (panel B), when (1) seed availability is limited by parent-tree abundance (unlikely to increase rapidly with warming); (2) fecundity at the range edge does not increase with warming; (3) germination decreases with climate change (due to climatic factors that become more limiting with climate change); and/or (4) germination is limited by competitive effects. Arrows under the microsite limitation graphs indicate the direction in which climatic factors will be altered by climate change.

fecundity at the range edge (Fig. 1A), then climate change may decrease seed limitation and facilitate range shifts as fecundity increases with warming climates (Case and Taper 2000). Studies estimate that as many as 50% of species' current potential ranges are not filled due to either low parent abundance, dispersal, or fecundity (e.g., Primack and Miao 1992, Ehrlén and Eriksson 2000, Turnbull et al. 2000, Myers and Harms 2009),

suggesting that seed limitation may have strong impacts on climate-change-induced range shifts.

Even when seeds are not limiting, the availability of suitable microsites for recruitment will influence responses to climate change (Clark et al. 1998, Caspersen and Saprundoff 2005). For example, at species' range limits, abiotic (e.g., climatic) factors, such as soil moisture and snowpack duration, may determine micro-



PLATE 1. Abiotic factors such as snow (which covers seedlings and limits the growing season at high elevations) likely constrain seedling recruitment at upper-elevational range limits of several conifer species in Mount Rainier National Park, Washington, USA. Photo credit: Kevin Ford, 14 July 2010.

site availability (see Plate 1; Franklin et al. 1988, Rochefort and Peterson 1996). If so, range expansions could be rapid if climate change renders those microsites more available (Fig. 1A; Case and Taper 2000, Adler and HilleRisLambers 2008). Alternatively, microsite availability may be affected by competitive effects from existing vegetation (Price and Kirkpatrick 2009). If so, climate-change-induced range shifts might be lagged since range expansions could be slowed by competing species (Thuiller et al. 2008). In contrast, suitable microsites defined by facilitative interactions (e.g., nurse plants) could have the opposite effect (HilleRisLambers et al. 2013). Thus, microsite limitation, and the abiotic and biotic factors that define suitable microsites, may further influence climate-change-induced range shifts.

Seed and microsite limitation may further interact in complex ways to influence species' responses to climate change. For one, the identity and strength of factors governing seed and microsite availability, and thus population growth rates at range edges, are likely to vary among species. As a result, recruitment responses to climate change could be species specific, with species with previously nonoverlapping ranges reassembling into novel communities (Gilman et al. 2010). Furthermore, annual variability in seed and microsite availabil-

ity, due to masting and temporally variable recruitment opportunities (Graber and Leak 1992, Sork et al. 1993), could also modulate climate-change-induced range shifts. For example, if years of high seed production are always followed by years with a greater availability of suitable microsites (e.g., earlier snow melt), then recruitment may not strongly constrain climate-change-induced range shifts. However, if seed availability and microsite suitability are uncorrelated (or negatively correlated), recruitment limitation may be magnified relative to expectations from each of these processes alone. Additionally, if years of high seed production are correlated among species and suitable microsites are shared, competitive interactions may also constrain recruitment.

Although studies have shown that seed and microsite limitation influence tree seedling recruitment (e.g., Clark et al. 1999), their relative importance in constraining climate-change-induced range shifts remains unknown. This is because few studies quantify seed and microsite limitation simultaneously (but see Eriksson and Ehrlén 1992, Clark 1998, Caspersen and Saprúnoff 2005). Moreover, most studies are short-term and occur over limited spatial scales, despite the fact that recruitment can be highly variable across years (Clark et al. 1999)



and over the large environmental gradients that encompass species' ranges (Sexton et al. 2009), both important factors when considering climate-change-induced range shifts.

To determine whether seed and microsite limitation may constrain the responses of trees to climate change, we therefore quantified seed availability and seedling recruitment (defined as successful germination) for five years across the elevational ranges of six dominant conifers in Mount Rainier National Park, Washington, USA. Specifically, we assessed (1) how tree abundance and annual variability in seed production (fecundity) affect seed availability; (2) how seed limitation varies across species' ranges; (3) how microsite conditions (climatic and biotic) affect germination; and (4) whether seed availability and microsite availability are temporally correlated within and among species. In combination, answering these questions allows us to speculate on how the factors constraining or facilitating recruitment may alter species' responses to climate change and whether species-specific differences in recruitment limitation may result in complex range shift dynamics. Recruitment limitation is common in forests (e.g., Clark et al. 1999) and focal tree species are known to mast, thus, we expected strong and annually variable seed limitation, especially at range limits. Snowfall strongly limits the growing season in the Pacific Northwest and, thus, we expected to find strong negative effects of snow duration on seed germination. We also expected germination to be affected by competition for light with surrounding vegetation, since light is one of the most limiting resources in forests (Price and Kirkpatrick 2009). We did not have strong expectations for how seed and microsite limitation would covary within and among species, but we did expect both would constrain recruitment, and thus, climate-change-induced range shifts.

## METHODS

### Site and species information

Our study occurred in the forest ecosystems of Mount Rainier National Park, located in the western Cascade Range in Washington, USA. The climate is temperate maritime, with a dry, warm season (June–September) and a wet, cool season (October–May; Rochefort and Peterson 1996). Mount Rainier spans large environmental gradients of temperature and precipitation across its elevational range (490–4392 m above sea level). Mean annual temperature in our study sites varies from 2.3°C to 8.0°C, cumulative annual precipitation varies from 125 to 277 cm, and snowpack duration varies from 30 to 300 days. Climate also varies considerably with aspect, as a result of the orographic effect, with growing season precipitation (June–September) on the eastern slope of the mountain being approximately 35% less than on the southwestern slope.

Forests on Mount Rainier are typified by closed canopy, old-growth (from 150 to  $\geq 1200$  years old), low-

diversity coniferous forests (16 canopy species; Franklin et al. 1988). We focus on six dominant species that are within the park (accounting for roughly 92% of tree abundance; Franklin et al. 1988) and are abundant in western Washington: *Abies amabilis* (Pinaceae), *Callitropsis nootkatensis* (Cupressaceae), *Pseudotsuga menziesii* (Pinaceae), *Thuja plicata* (Cupressaceae), *Tsuga heterophylla* (Pinaceae), and *Tsuga mertensiana* (Pinaceae). We categorize these species into two groups: treeline species (whose upper range edges occur near the treeline; *Callitropsis nootkatensis*, and *Tsuga mertensiana*) and mid/lower elevation species (whose upper range edges occur in closed-canopy forests; *Abies amabilis*, *Pseudotsuga menziesii*, *Thuja plicata*, and *Tsuga heterophylla*).

We studied recruitment limitation for the aforementioned six species in 18 forest stands spanning a broad range of environmental conditions and community compositions (Appendix A). Fifteen of these stands were established as part of the Permanent Sample Plot Network (PSP) in the late 1970s (Dyrness and Acker 2000). The remaining three stands were established between 2009 and 2010 at higher elevations than the PSP plots to more fully encompass the upper elevational range limits of several focal species. We categorized each stand as falling into the lower, core, or upper third of species' ranges (Appendix A: Fig. A2). We measured the diameter at breast height (dbh; 1.4 m aboveground) of every stem  $>15$  cm dbh in a  $25 \times 50$  m area at each stand (Appendix A).

### Seed and seedling censuses

We assessed seed production and germination rates annually from 2009 to 2013, (except for the three high-elevation stands, where sampling was initiated in 2010 or 2011). We censused seed production using six 0.176-m<sup>2</sup> seed traps spaced 5 m apart along a linear transect in the center of each of the  $25 \times 50$  m forest stands (Appendix A). Seed traps were lined with mosquito netting to capture seeds ( $\sim 0.5$ -mm mesh size, smaller than our focal species' seeds) and covered with chicken wire to deter rodent herbivory. Seed production occurs in the fall and dispersal occurs throughout fall and winter; thus, we collected seed trap contents each spring after snowmelt to capture all seeds produced the previous fall. All seeds were identified to species and counted. To estimate germination rates, we censused seedlings in a 1-m<sup>2</sup> plot adjacent to each seed trap (Appendix A: Fig. A1) once peak germination had occurred, approximately three weeks after snowmelt. Since other studies have shown that seeds are only viable for one year (i.e., no long term seedbank; Bonner and Karrfalt 2008), we calculated germination rates for each plot by dividing the number of seedlings in each plot by the number of seeds per m<sup>2</sup> estimated from seed densities in the adjacent seed trap in the previous year.

### Microsite conditions

To assess microsite conditions in seedling plots, we annually quantified climatic and biotic factors that could influence germination: snowpack duration, soil moisture (climatic factors likely to be influenced by climate change), canopy density, and percent cover of understory plants (both proxies for intra- and inter-specific competitive interactions, primarily for light). We quantified snowpack duration using HOBO temperature loggers (Onset Computer; Bourne, Massachusetts, USA; Appendix B), and we quantified soil moisture with Decagon Devices ECH<sub>2</sub>O soil moisture probes (Decagon Devices, Pullman, Washington, USA) and estimated missing values (gap-filling due to sensor failures; see Appendix B). We used a spherical canopy densiometer to measure percent canopy cover at four locations within each plot each census (Lemmon 1956) and estimated percent cover of all understory plants in each plot. Several microclimate explanatory variables were correlated (Appendix D: Table D2); however, all correlations were less than 0.2. Variance inflation factors in all germination models were all less than the recommended cutoff of 2 (Zuur et al. 2009). Thus, we chose to include all microsite parameters in model fitting.

### Analyses for seed limitation

We used linear mixed-effects models to examine how seed density is limited by parent-tree abundance and annual variability in seed production for each species. We examined a range of models with effects of parent-tree abundance and year for model selection (Appendix C), but here only describe the most complex model (Eq. 1). We modeled seed density for plot  $i$  in stand  $j$  in year  $t$  following a negative binomial distribution (with log link) with mean  $\mu_{ijt}$

$$\log(\mu_{ijt}) = \alpha_0 + \alpha_1 \text{Basal.area}_j + \alpha_2 \text{Year}_t + \alpha_3 \text{Basal.area}_j \text{Year}_t + b_j \quad (1)$$

where  $\text{Basal.area}_j$  is parent-tree basal area in stand  $j$ ,  $\text{Year}_t$  is census year,  $\alpha$  terms are estimated parameters ( $\alpha_0$  is an intercept term), and  $b_j$  is a random effect of stand. We used a negative binomial rather than a Poisson distribution because seed density data were overdispersed. We also included an intercept term,  $\alpha_0$ , in all models to account for long-distance dispersal events (i.e., seeds present but parent trees absent). These models were fit using the glmmADMB package in the R programming language (version 3.0.1; R Development Core Team 2013).

### Analyses for seed limitation across species' ranges

We examined how seed limitation varied across each species' range by asking whether range position influenced seed densities, parent-tree abundance, and fecundity. We defined fecundity as per capita seed production, i.e., seed production (seeds per seed trap) divided by

conspecific basal area in that stand. For these analyses, we only included data for stands in which parent trees were present. We modeled seed density and fecundity for plot  $i$  in stand  $j$  in year  $t$  with a negative binomial (for seeds) or normal (for fecundity) distribution with mean  $\mu_{ijt}$

$$\log(\mu_{ijt}) = \alpha_0 + \alpha_1 \text{Range}_j + b_j + c_t \quad (2)$$

where  $\text{Range}_j$  is the range position for stand  $j$ ,  $b_j$  is a random effect of stand, and  $c_t$  is a random effect of year. The  $\alpha$  terms are estimated parameters ( $\alpha_0$  is an intercept term). Three error terms (seed trap level, stand level, and year level) were also fit for these models.

To assess whether range position influenced parent-tree abundance, we modeled parent-tree basal area for stand  $j$  following a normal distribution with mean  $\mu_j$

$$\mu_j = \alpha_0 + \alpha_1 \text{Range}_j \quad (3)$$

where  $r_j$  is the range position for stand  $j$ . However, since there is only one measure of total parent-tree abundance per stand, we do not include random effects of stand or year in this model.

### Analyses for microsite limitation

To assess how germination is limited by microsite availability, we determined how germination is influenced by climate vs. competitive explanatory variables. We did this by fitting models including all or a subset of microsite explanatory variables and performing model selection (Appendix C). We did not fit models with interactions, as we were most interested in effect size differences. We only describe the most complex model we fit (Eq. 4). We used a linear mixed-effects logistic regression with a binomial error distribution (and logit link) to fit models of germination rate for plot  $i$  in stand  $j$  in year  $t$  with mean  $\mu_{ijt}$

$$\text{logit}(\mu_{ijt}) = \alpha_0 + \alpha_1 \text{Snow}_{ijt} + \alpha_2 \text{Soilm}_{ijt} + \alpha_3 \text{Canopy}_{ijt} + \alpha_4 \text{Understory}_{ijt} + b_j + c_t \quad (4)$$

where  $\text{Snow}_{ijt}$  is snowpack duration,  $\text{Soilm}_{ijt}$  is soil moisture,  $\text{Canopy}_{ijt}$  is canopy cover,  $\text{Understory}_{ijt}$  is understory plant cover,  $\alpha$  terms are estimated parameters ( $\alpha_0$  is an intercept term),  $b_j$  is a stand random effect, and  $c_t$  is a year random effect.

The number of seeds available for germination in each plot (i.e., the size in a binomial trial) was estimated from seed counts in adjacent traps, scaled to 1 m<sup>2</sup>, and rounded to the nearest whole number. Note that we only examined germination probability for plots that had seeds for the relevant species in the adjacent seed trap. However, sometimes seedlings were found when no seeds for the associated species were located in the adjacent seed trap. In these cases (9.7% of the germination data set), we assumed 100% germination rates with seeds available for germination set to the number of seedlings found (as in HilleRisLambers et al. 2002). We verified that results were qualitatively similar

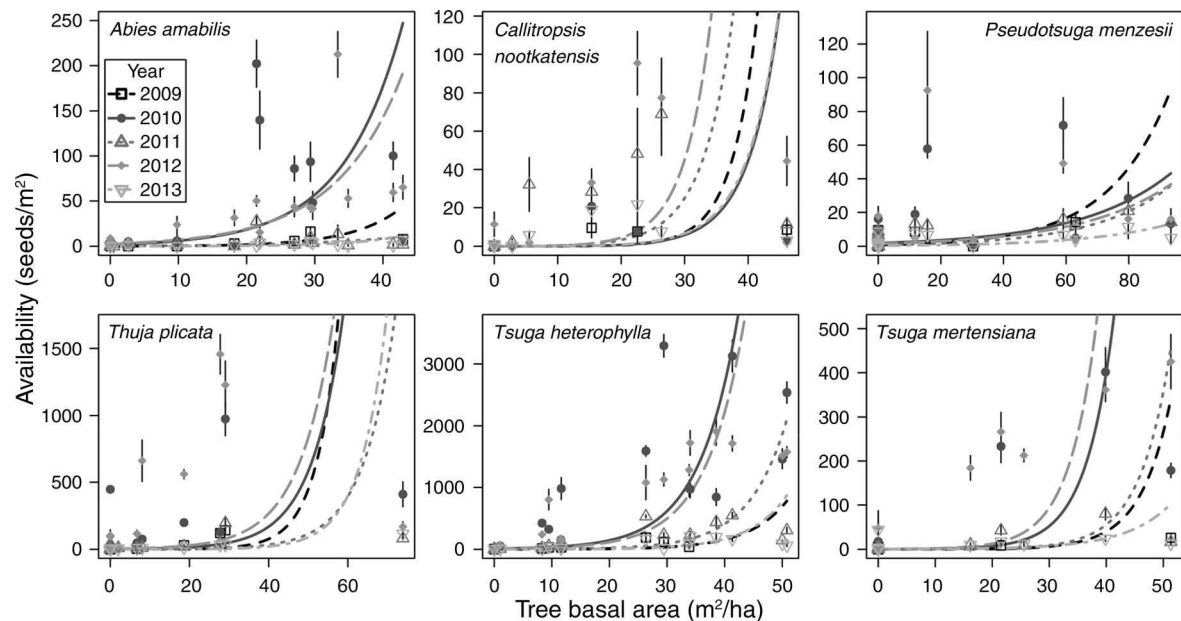


FIG. 2. Seed availability is related to parent-tree basal area, but also exhibits considerable annual variation. Points with error bars represent the year-specific mean and SE of seed densities across the six seed traps within each forest stand, with symbol shapes and line types differing by year. Seeds/m<sup>2</sup> refers to the sampling plot.

when we excluded these observations and repeated analyses. All microclimatic predictors were standardized and centered prior to analysis for the ease of interpretation. These models were fit using the glmer function in the lme4 package in R.

#### *Analyses for temporal variation and correlations in seed availability and microsite limitation*

We examined temporal correlations between seed availability and microsite availability within and among species. To do this, we first used Pearson correlation coefficients to estimate the strength of association between annual seed availability and germination rates within each stand (averaged across plots within stands that had at least three years of seed and microsite data). We then used one-sample *t* tests to determine if mean correlation coefficients (one per stand) differed from zero at the species level (i.e., across all the stands where a species occurred). To examine whether species mast at the same time, we examined the strength of association between mean annual seed availability for pairs of co-occurring species with Pearson correlation coefficients (averaged across plots within stands with at least three years of seed data). We then used *t* tests to determine whether or not the mean correlation coefficient significantly differed from zero for each pair of species (i.e., across all stands where those species co-occurred).

#### *Seed viability: implications for results and conclusions*

We did not quantify seed viability, which could vary by stand and year (but is unlikely to vary among seed traps within a stand due to their proximity to each other). Seed

viability that varies directionally across species ranges (e.g., declining with elevation) could theoretically contribute to associations between microsite conditions that also vary by elevation (e.g., snow duration) and germination rates. Seed viability that varies by year (and in particular, is associated with mast) could also theoretically affect temporal correlations in seed production (between species) and between seed production and microsite availability (within species). However, additional analyses and data (collected during another study; A. K. Ettinger, unpublished data) suggest our qualitative conclusions about microsite effects on germination and temporal patterns in seed and microsite availability were not influenced by our lack of information on seed viability, as explained in Appendix E.

## RESULTS

### *Seed limitation*

Plot-specific seed densities were positively related to conspecific tree basal area, suggesting seed availability is limited by parent-tree abundance. However, the relationship between basal area and seed density varied annually (Fig. 2), with seed densities varying annually by as much as two orders of magnitude. Best-fitting models for all species included parent-tree abundance, year, and their interaction (Appendix C), with the exception of *Pseudotsuga menziesii*, where the model with only year was within 2 Akaike's information criterion (AIC) units of the full model.

Model fits of seed availability were sometimes poor (Fig. 2), and several factors may have contributed to this. First, the log-linear relationship assumed by our

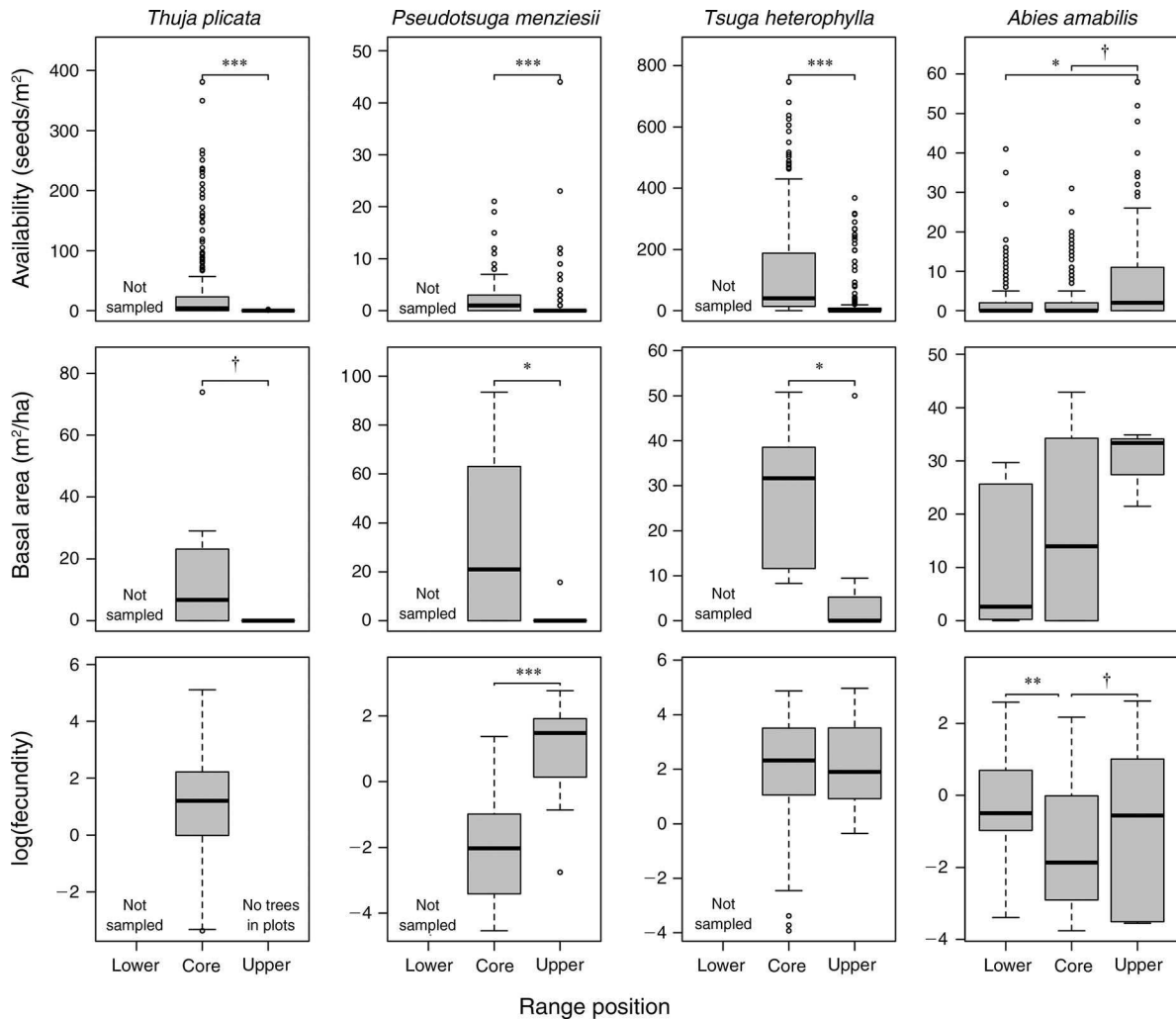


FIG. 3. Seed availability, parent-tree abundance (basal area), and log-transformed fecundity per unit parent-tree basal area across species' ranges. Analyses are limited to stands where trees were present. The lower ranges of some species extend below our study area and are therefore not sampled. Boxes indicate the interquartile range (25th to 75th percentile) and the line shows the median. Error bars show  $\pm 1.5$  times the interquartile range to the 25th and 75th percentiles, respectively. Outlier points are beyond 1.5 times the interquartile range  $\pm$  the 25th and 75th percentiles, respectively. Horizontal bars group range positions by significance levels: †  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

model may not be the most appropriate. Second, basal area in a  $25 \times 50$  m plot is a fairly imprecise measure of the trees contributing seeds to seed traps, considering trees can be spatially aggregated, dispersal distances can differ among species, and individuals may differ in reproductive status. While both factors contribute noise to the relationship between basal area and seed availability, neither likely alters our conclusion that seed availability is linked to tree abundance and varies enormously annually.

#### Seed limitation across species' ranges

Seed availability was lower at range edges than the range core for four of the six upper range edges and two of the three lower range edges (Fig. 3). However, two species (*Abies amabilis* and *Tsuga mertensiana*) had

higher seed densities at upper range edges. Differences in seed availability across species' ranges resulted from differences in basal area rather than fecundity, as fecundity (seeds per conspecific basal area) did not vary strongly with range position (Fig. 3, but see *Abies amabilis* and *Pseudotsuga menziesii*).

#### Microsite limitation

For all species, models with all climatic and competitive variables best explained the data (Appendix C). However, the significance and direction of effect of microsite variables on germination varied by species (Fig. 4; Appendix D: Table D1). For example, snowpack duration positively affected germination for two species (*Abies amabilis*, *Thuja plicata*) and negatively affected germination for three species (*Callitropsis nootkatensis*,



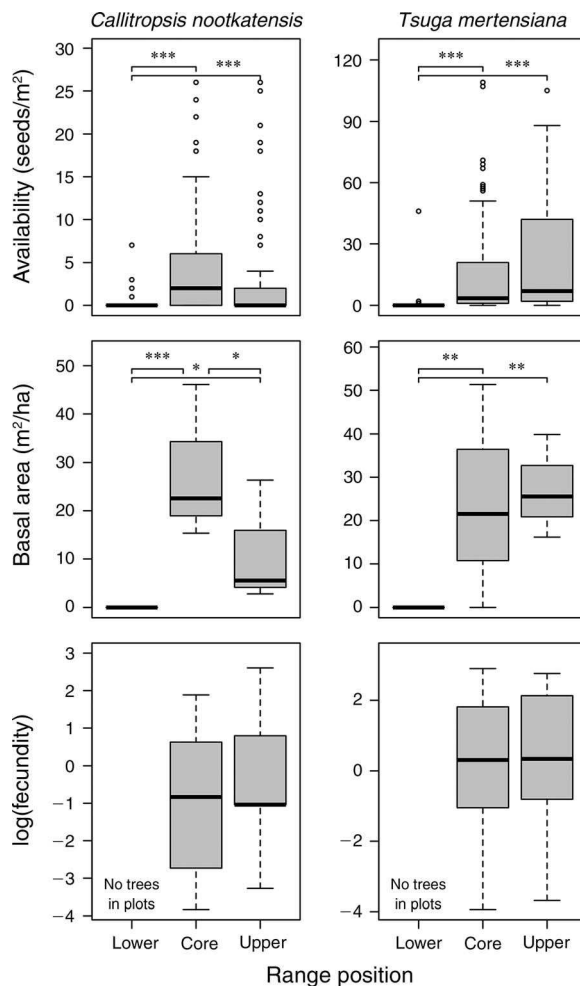


FIG. 3. Continued.

*Tsuga heterophylla*, *Tsuga mertensiana*). Canopy density had consistently negative effects on all species except for *Abies amabilis*. Snowpack duration and canopy density generally had much larger overall effects on germination than did soil moisture and understory plant cover (Fig. 4). Furthermore, the effects of soil moisture and understory cover were only significant for two and four species, respectively.

#### Temporal variation and correlations in seed availability and microsite limitation

Seed density and germination fraction (a function of microsite limitation) were not temporally correlated within species, with the exception of *Tsuga heterophylla* (Fig. 5). Species tended to mast concurrently, as seed density between species pairs was frequently correlated (Appendix D: Table D3), with masting events occurring in 2010 and 2012 (Fig. 5). While approximately half of the pairwise correlations were not significant, all but one was positive, suggesting that high seed availability years tend to occur concurrently for focal species.

#### DISCUSSION

Our results indicate that recruitment limitation through seed and microsite availability will constrain the ability of these long-lived conifers to track shifting climatic conditions and add complexities to climate-change-induced range shifts. Several lines of evidence lead to this conclusion. Seed availability tended to decline toward species' upper range edges due to low parent-tree abundance. This suggests that warming is unlikely to increase seed availability at range edges unless adult-tree densities increase. Additionally, germination rates were sensitive to snowpack duration and canopy density in a species-specific manner, and both are factors likely to change in a future warming world. Furthermore, germination rates of treeline and lower elevation species differed in their responses to snowpack duration and canopy cover, implying faster upward range shifts for treeline species than for low-elevation species. Finally, seed production and germination rates were highly variable across years but uncorrelated, suggesting successful recruitment (requiring available seeds and successful germination) can be a rare event. Future recruitment frequency may vary among species due to species-specific responses to climate change in terms of masting frequency and/or microsite availability.

#### Seed limitation and its role during climate-change-induced range shifts

In all, our data suggest that range expansions will be strongly limited by seed availability. We found that fecundity (seeds/basal area) does not vary with elevation, implying that seed densities at range edges are low due to low adult-tree abundances rather than decreased fecundity (Figs. 2 and 3). If climate indeed does not influence the fecundity of these species, warming climates may not immediately alleviate recruitment limitation because changes in adult density are likely to be slow. Our focal species have long generation times (Verdú 2002, Bonner and Karrfalt 2008), which means that increases in the density of reproductive adults are likely to lag changing climates. For example, Grace and colleagues (2002) estimated that range expansions at treeline might only advance at one-sixth the pace of isotherm shifts due to generation time lags.

However, the degree to which seed availability limits range expansions will likely vary by species (Fig. 3). For example, basal area and total seed availability of *Abies amabilis* actually increased toward the leading range edge. We do not believe these patterns reflect rapid responses to recent warming, as even saplings of this species are typically around 100 years old (Ettinger and HilleRisLambers 2013). Instead, basal area of *A. amabilis* may be high at its upper range edge due to increased competition at lower elevations or another unknown factor. Regardless, climate induced range expansions may occur much more quickly for this species, since seed availability is less limiting at its upper range edge than the other species in our study.



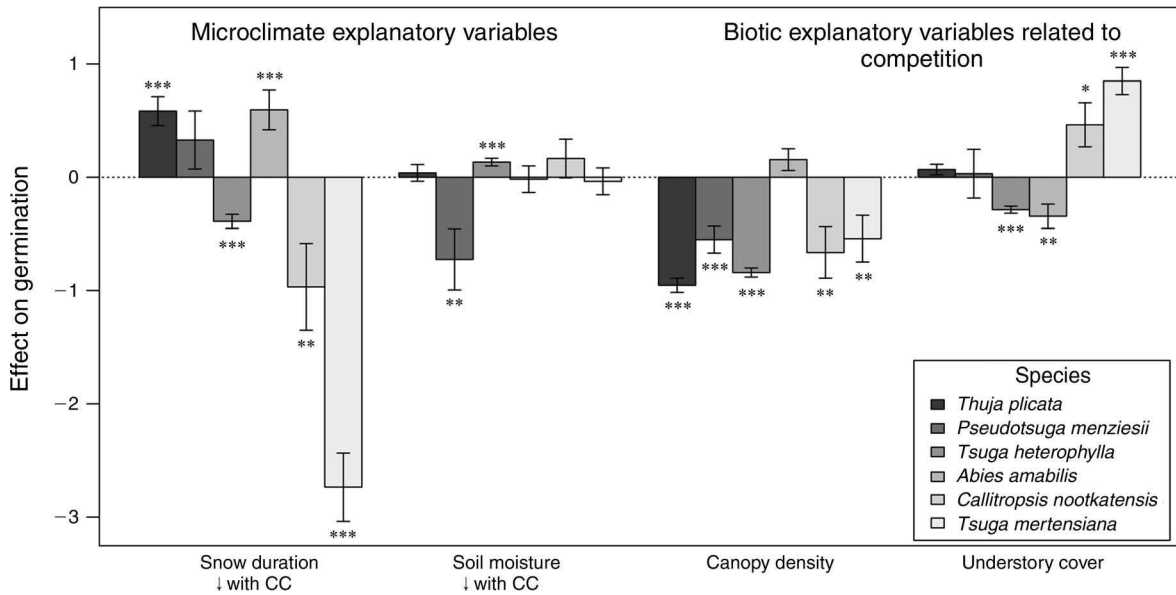


FIG. 4. Effects of abiotic (snowpack duration and soil moisture; both predicted to decline with climate change, CC) and biotic (canopy density and understory percent cover) microclimate variables on germination rates. All variables were standardized prior to analysis, making the height of different bars directly comparable. Species are ordered from left to right by increasing elevation of their range center. Error bars represent  $\pm$ SE. Significance from the full models (including all explanatory variables) is indicated as: \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

Although our results suggest the fecundity of these species does not vary across the strong environmental gradients of our study or with range position, and therefore, is not influenced by climate (Fig. 3), climate change may influence masting dynamics. Variation in annual seed availability spanned almost two orders of magnitude (Fig. 5), which was expected since several of our study species are known to mast (Koenig and Knops 1998). Since masting has been shown to be tied with high temperatures (Sork et al. 1993), shifts in the mean and variability of global surface temperatures could alter masting frequency. For some species, this might be beneficial for range expansion, as has been recently demonstrated (McKone et al. 1998). In other cases, increases in the variability of seed production may cause recruitment to be increasingly episodic, since years for high germination do not necessarily follow masting events (Fig. 5). However, with only five years of data, we were unable to assess whether annual variability in seed production was directly linked to climate.

Species' responses to climate change may be further complicated by community masting events, since annual seed production appears to be synchronous for at least one-half of the species pairs (Fig. 5; Appendix D: Table D3). On one hand, community masting events may increase seedling recruitment via predator satiation (Silvertown 1980). On the other, there may be strong interspecific competition among seedlings during common masting years. Although competition between seedlings is generally thought to be weak in closed canopy forests (Paine et al. 2008), competition can intensify in tree-fall gaps where seedling densities can

become extremely high, particularly after community masting events (Taylor and Aarssen 1989). Thus, the competitive outcomes between species recruiting in tree-fall gaps after masting events (when seed availability may be less limiting) may additionally constrain range expansions of focal species and determine future forest community compositions.

#### *Microsite limitation and its role during climate-change-induced range shifts*

Microsite availability is likely to constrain range shifts of focal species' responses (Fig. 4), with species-specific effects, implying complex and difficult to predict range shifts. For example, snowpack duration, which had strong impacts on germination (Fig. 4), is projected to decline with climate change in the Pacific Northwest (Salathé et al. 2010). Germination in one-half of our focal species was negatively affected by greater snow duration, implying that these species will not see increased germination at range edges with climate change. Soil moisture and understory cover had similarly species-specific effects on germination of our focal species (Fig. 4). Even the one explanatory variable that had consistent impacts on germination of our focal species (the negative impacts of canopy density) will be difficult to predict, as changes to canopy density with warming are uncertain (HilleRisLambers et al. 2013). Finally, other microsite limiting factors not assessed in this study could modulate climate change responses, thereby limiting the accuracy of our predictions. For example, range shifts may allow species to encounter novel abiotic conditions (e.g., soil types) or species

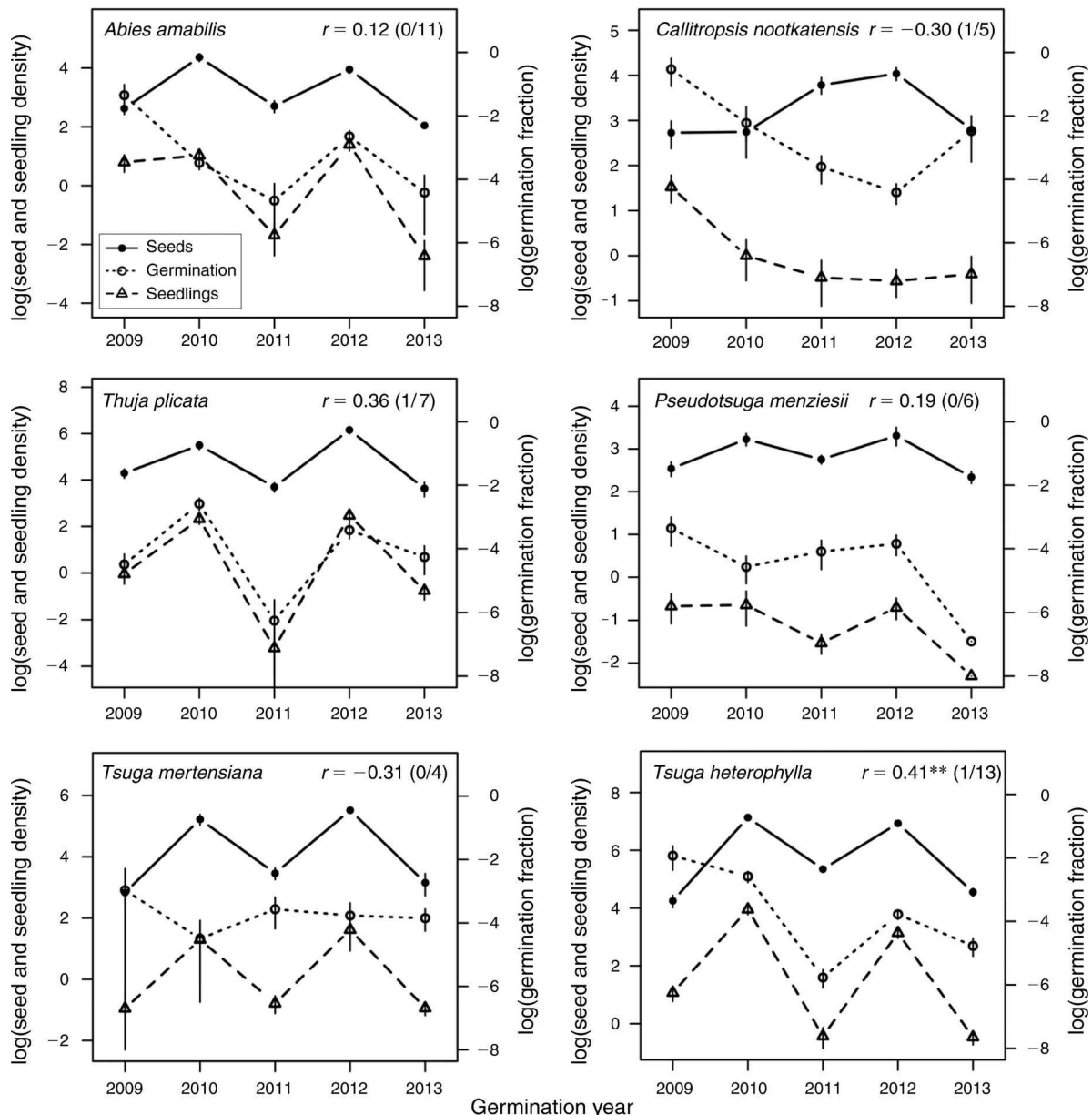


FIG. 5. Annual variability in seed and seedling density (left axis), germinant density (left axis) and germination fraction (right axis) for all focal species. Values have been log-transformed to facilitate comparison between annual patterns. Symbols represent means  $\pm$  SE across all stands where seeds were present. Panels are ordered by increasing elevation of the species' range center from left to right, starting at the bottom left. Correlation estimates ( $r$ ) indicate species-level correlation coefficients (across all stands in which a species was present) among seed density and germination fraction; asterisks indicate significance levels (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ). Numbers in parentheses indicate the fraction of individual stand-level correlations that are significant (out of the number of stands in which a species is present). Seeds/m<sup>2</sup> refers to the sampling plot.

interactions (e.g., seed predators, soil mutualists) further constraining or facilitating species range shifts (Gilman et al. 2010).

Our data suggest that microsite limitation may more strongly constrain the ability of low-elevation focal species to expand their upper elevational ranges with warming than high elevation species. Snowpack duration had positive effects on germination rates of low- and mid-

elevation species, *Thuja plicata* and *Abies amabilis*, but strong negative effects on germination rates of the high elevation species, *Callitropsis nootkatensis* and *Tsuga mertensiana* (Fig. 4). Long snowpack durations may influence germination rates by limiting seed desiccation or seed predation, increasing soil moisture during germination, or decreasing growing season length. Regardless of the mechanism, this suggests that expected snowpack

declines in the Pacific Northwest (Salathé et al. 2010) will negatively affect germination of the low-elevation species, but positively affect germination of the high-elevation species. Furthermore, canopy cover tended to have large and negative impacts on seed germination for all species (Fig. 4), while germination of the high-elevation species was positively affected by understory cover (potentially indicating facilitation; Callaway et al. 2002). Thus, recruitment of low-elevation species above their range edges, in closed canopy forests, could be slow, unless tree mortality increases sharply. Conversely, recruitment of high-elevation species may be fast, since canopy cover is low and understory cover is high in the alpine meadows above their upper ranges, which occur near treeline. These projections are supported by studies demonstrating that alpine meadows may be less resistant to invasion than closed-canopy forests (Dullinger et al. 2004).

### Conclusions

Understanding future forests in a warming world requires that we determine which vital rates will constrain climate-change-induced range shifts. Unfortunately, recruitment, likely to play a major role during range expansions, is understudied in trees, perhaps because adult survival is a major contributor to population dynamics of long-lived tree species at equilibrium. We use extensive spatiotemporal data collected across large environmental gradients to demonstrate that seed and microsite limitation are likely to be critical bottlenecks during range expansions of focal trees. Because we studied altitudinal range limits (where distances to newly suitable habitat with warming are low), we expect latitudinal range shifts of conifer species in the Pacific Northwest to be even more constrained by recruitment, especially with the unprecedented rates of climate change projected in the next century. Additionally, we found species-specific differences in the strength and nature of seed and microsite limitation, implying idiosyncratic range shifts that could lead to novel future forest communities. In all, our results provide strong support for studies of range-wide demographics (e.g., Doak and Morris, 2010) as a way to anticipate the complexities of climate change induced range shifts.

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### LITERATURE CITED

- Adler, P. B., and J. HilleRisLambers. 2008. The influence of climate and species composition on the population dynamics of ten prairie forbs. *Ecology* 89:3049–3060.
- Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications* 1:95–111.
- Bonner, F., and R. Karrfalt. 2008. The woody plant seed manual. United States Department of Agriculture, Forest Service, Washington, D.C., USA.
- Callaway, R., R. Brooker, P. Choler, Z. Kikvidze, C. L. Lortie, R. Michalet, L. Paolini, F. Pugnaire, B. Newingham, E. Aschehoug, C. Armas, D. Kikodze, and B. Cook. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417:844–848.
- Case, T., and M. Taper. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *American Naturalist* 155:583–605.
- Caspersen, J., and M. Saprunoff. 2005. Seedling recruitment in a northern temperate forest: the relative importance of supply and establishment limitation. *Canadian Journal of Forest Research* 35:978–989.
- Clark, J., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs* 68:213–235.
- Clark, J. S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist* 152:204–224.
- Clark, J. S., B. Beckage, P. Camill, B. Cleveland, J. HilleRisLambers, J. Lichter, J. McLachlan, J. Mohan, and P. Wyckoff. 1999. Interpreting recruitment limitation in forests. *American Journal of Botany* 86:1–16.
- Daly, C., M. Halbleib, J. Smith, W. Gibson, M. Doggett, G. Taylor, J. Curtis, and P. Pasteris. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology* 28:2031–2064.
- Dovčiak, M., P. Reich, and L. Frelich. 2003. Seed rain, safe sites, competing vegetation, and soil resources spatially structure white pine regeneration and recruitment. *Canadian Journal of Forest Research* 33:1892–1904.
- Dullinger, S., T. Dirnböck, and G. Grabherr. 2004. Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. *Journal of Ecology* 92:241–252.
- Dullinger, S., and K. Hülber. 2011. Experimental evaluation of seed limitation in alpine snowbed plants. *PLoS ONE* 6.
- Dyrness, T., and S. Acker. 2000. Permanent plots in the Mount Rainier National Park. Permanent plots of the PNW. Report Number 4. Oregon State University, Corvallis, Oregon, USA.
- Ehrlén, J., and O. Eriksson. 2000. Dispersal limitation and patch occupancy in forest herbs. *Ecology* 81:1667–1674.
- Eriksson, O., and J. Ehrlén. 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia* 91:360–364.
- Ettinger, A. K., and J. HilleRisLambers. 2013. Climate isn't everything: competitive interactions and variation by life stage will also affect range shifts in a warming world. *American Journal of Botany* 100:1344–1355.
- Ford, K. R., A. K. Ettinger, J. D. Lundquist, M. S. Raleigh, and J. Hille Ris Lambers. 2013. Spatial heterogeneity in ecologically important climate variables at coarse and fine scales in a high-snow mountain landscape. *PLoS ONE* 8: e65008.
- Franklin, J., W. H. Moir, M. A. Hemstrom, S. E. Greene, and B. G. Smith. 1988. The Forest Communities of Mount Rainier National Park. United States Department of the Interior, National Park Service, Washington, D.C., USA.
- Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. *Trends in Ecology and Evolution* 25:325–31.
- Graber, R., and W. Leak. 1992. Seed fall in an old-growth northern hardwood forest. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA.

- Grace, J. 2002. Impacts of climate change on the tree line. *Annals of Botany* 90:537–544.
- Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters* 12:1040–1049.
- HilleRisLambers, J., J. S. Clark, and B. Beckage. 2002. Density-dependent mortality and the latitudinal gradient in species diversity. *Nature* 417:732–735.
- HilleRisLambers, J., M. A. Harsch, A. K. Ettinger, K. R. Ford, and E. J. Theobald. 2013. How will biotic interactions influence climate change-induced range shifts? *Annals of the New York Academy of Sciences* 1297:112–125.
- Jones, C. C., and R. Moral. 2009. Dispersal and establishment both limit colonization during primary succession on a glacier foreland. *Plant Ecology* 204:217–230.
- Koenig, W., and J. Knops. 1998. Scale of mast-seeding and tree-ring growth. *Nature* 396:225–226.
- Lemmon, P. 1956. A spherical densimeter for estimating forest overstory density. *Forest Science* 2:314–320.
- McKone, M., D. Kelly, and W. Lee. 1998. Effect of climate change on mast-seeding species: frequency of mass flowering and escape from specialist insect seed predators. *Global Change Biology* 4:591–596.
- Myers, J. A., and K. E. Harms. 2009. Seed arrival, ecological filters, and plant species richness: a meta-analysis. *Ecology Letters* 12:1250–1260.
- Nathan, R., and H. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15:278–285.
- Paine, C. T., K. Harms, S. Schnitzer, and W. Carson. 2008. Weak competition among tropical tree seedlings: implications for species coexistence. *Biotropica* 40:432–440.
- Platt, W., G. Evans, and S. Rathbun. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). *American Naturalist* 131:491–525.
- Price, T. D., and M. Kirkpatrick. 2009. Evolutionarily stable range limits set by interspecific competition. *Proceedings of the Royal Society B* 276:1429–1434.
- Primack, R. B., and S. L. Miao. 1992. Dispersal can limit local plant distribution. *Conservation Biology* 6:513–519.
- R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [www.r-project.org](http://www.r-project.org)
- Raleigh, M. S., K. Rittger, C. E. Moore, B. Henn, J. A. Lutz, and J. D. Lundquist. 2013. Ground-based testing of MODIS fractional snow cover in subalpine meadows and forests of the Sierra Nevada. *Remote Sensing of Environment* 128:44–57.
- Rocheftort, R., and D. Peterson. 1996. Temporal and spatial distribution of trees in subalpine meadows of Mount Rainier National Park, Washington, USA. *Arctic and Alpine Research* 28:52–59.
- Salathé, E. P., L. R. Leung, Y. Qian, and Y. Zhang. 2010. Regional climate model projections for the State of Washington. *Climatic Change* 102:51–75.
- Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics* 40:415–436.
- Silvertown, J. 1980. The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnean Society* 14:235–250.
- Sork, V., J. Bramble, and O. Sexton. 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. *Ecology* 74:528–541.
- Stueve, K. M., R. E. Isaacs, L. E. Tyrrell, and R. V. Densmore. 2011. Spatial variability of biotic and abiotic tree establishment constraints across a treeline ecotone in the Alaska range. *Ecology* 92:496–506.
- Taylor, K., and L. Aarssen. 1989. Neighbor effects in mast year seedlings of *Acer saccharum*. *American Journal of Botany* 76:546–554.
- Thuiller, W., C. Albert, M. B. Araújo, P. M. Berry, M. Cabeza, A. Guisan, T. Hickler, G. F. Midgley, J. Paterson, F. M. Schurr, M. T. Sykes, and N. E. Zimmermann. 2008. Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics* 9:137–152.
- Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88:225–238.
- Verdú, M. 2002. Age at maturity and diversification in woody angiosperms. *Evolution* 56:1352–1361.
- Zuur, A., E. Ieno, N. Walker, A. Saveliev, and G. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

## SUPPLEMENTAL MATERIAL

## Ecological Archives

Appendices A–E are available online: <http://dx.doi.org/10.1890/14-0595.1.sm>