



Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States

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ABSTRACT

Aim To determine if differences in climate envelopes for six coniferous tree species and two life stages (trees and seedlings) suggest a potential for species range contractions, expansions or shifts in response to climate change and if these patterns differ between subalpine (i.e. cool-climate) and montane (i.e. warm-climate) species.

Location The dry domain of the western United States.

Methods Using data from the Forest Inventory and Analysis National Program, we quantified the relationship between probability of occurrence and climate for adults and seedlings of each species with a Bayesian logistic regression. Assuming that distributional differences between life stages highlight shifting regeneration patterns relative to adult trees, we assessed differences between seedlings and adult trees based on predicted probabilities of occurrence and climate envelope boundaries.

Results Differences between occurrence probabilities for seedlings and adults were greatest for montane, as opposed to subalpine, species and along range margins, especially in the southern and western portions of the study area. Climate envelope boundaries of seedlings differed from adult trees most frequently in montane species and often suggested range contractions or range shifts, as opposed to range expansion.

Main conclusions Our results indicated that climate-induced contractions and shifts in seedling distribution in response to recent change are already under way and are particularly severe in montane tree species. While adult trees may persist for hundreds of years without significant regeneration, tree species ranges will eventually contract where tree regeneration fails.

Keywords

Biogeography, climate envelope models, life stages, range shift, tree regeneration, western United States.

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INTRODUCTION

The migration and persistence of tree species under climate change depend on successful regeneration, and persistent disparities in distribution between life stages may be an early indicator of impending range shifts. Given that the temperature and precipitation regimes of the western United States are anticipated to change substantially during the 21st century (Christensen *et al.*,

2007; MacDonald, 2010; Seager & Vecchi, 2010) and that climatic shifts are already modifying forest structure and function (Breshears *et al.*, 2005; van Mantgem *et al.*, 2009; Allen *et al.*, 2010; Ma *et al.*, 2012), studies of the biogeographical controls on the distributions of tree species are critically important. With such dramatic changes, we must improve our understanding of processes determining leading and trailing range margin dynamics (Thuiller *et al.*, 2008), such as tree regeneration. Failures in

reproduction or regeneration, especially at range margins, may determine the persistence or migration of species in the face of climate change (Clark, 1998; Morin *et al.*, 2007; Clark *et al.*, 2011). Differences in climatic requirements for adult survival versus regeneration can result in regional regeneration failures, and have influenced past changes in species distributions in the dry forest systems of the western United States (Jackson *et al.*, 2009). While it has long been recognized that the regeneration and adult survival niches are expected to differ somewhat (Grubb, 1977), large discrepancies between the climatic conditions associated with adult trees and earlier life stages across regions imply the potential for future contractions, expansions or shifts.

Despite the importance of tree regeneration in determining species distributions, the impact of climate change on seedling biogeography remains uncertain. Studies of the distributional responses of seedlings along elevational and latitudinal gradients provide evidence of upslope or northward migration (Vitasse *et al.*, 2012) as well as range contraction (Zhu *et al.*, 2012) in response to recent climate change. Though distributional responses are mediated by non-climatic factors (e.g. dispersal; Lesser & Jackson, 2012), examinations at broad scales can provide important insights into shifting species ranges (Pearson & Dawson, 2003), particularly when large distributed networks of sampling plots are available (Boucher-Lalonde *et al.*, 2012). For example, narrow climate envelopes imply greater sensitivity to climate change (Thuiller *et al.*, 2005). Furthermore, one might expect reductions in seedling occurrence relative to tree occurrence at range margins that have experienced recent climate change because seedlings should be more sensitive to environmental stressors (e.g. drought) than adult trees (Cavender-Bares & Bazzaz, 2000). Therefore, quantifying the climate envelopes for differing life stages across broad, multidimensional environmental gradients (e.g. Bertrand *et al.*, 2011) may provide an appropriate framework for assessing the potential impacts of climate change on tree regeneration.

The examination of potential changes in biogeography requires that the aspects of climate being examined should be both influential and in the process of changing. The interpretation of the distributional responses of trees to climate change is complicated by the inadequate representation of complex climatic conditions (Austin, 2002). In the case of tree species distributions in western North America, the mean and seasonality of temperature and precipitation are particularly important (Shafer *et al.*, 2001; Rehfeldt *et al.*, 2006; Schrag *et al.*, 2008). Temperatures increased across much of the western United States during the 20th century, while increases and decreases in precipitation and temperature seasonality were observed (Fig. 1). Such broad-scale geographic variation is also expected under predicted 21st century climate change across the region (Christensen *et al.*, 2007). Therefore, we assume that the examination of differences in life-stage distributions with respect to mean and seasonality in temperature and precipitation will provide valuable insights into potential future changes in distribution.

Forest inventories have been used to characterize tree and seedling biogeography in North America and Europe (Lenoir

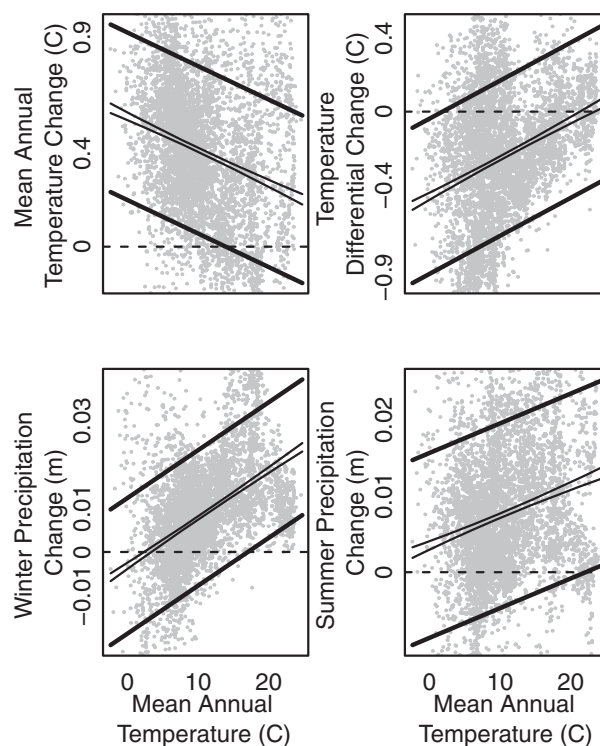


Figure 1 Observed climatic deviations (gray shading), 95% confidence intervals (thin black lines) and 95% predictive intervals (bold black lines) in (a) mean annual temperatures, (b) temperature differential (i.e. the difference between summer and winter temperatures), (c) winter precipitation, and (d) summer precipitation between the 115-year average (1895–2010) and the most recent 30 years (1981–2010) for 10,000 randomly selected 5-km grid cells in the dry domain of the United States.

et al., 2009; Woodall *et al.*, 2009; Bertrand *et al.*, 2011; Zhu *et al.*, 2012), although nearly all studies have focused on humid, temperate forest systems. This study used data from the US Forest Service Forest Inventory and Analysis National Program (FIA), an extensive forest inventory, to address the potential influence of differences in adult and seedling climate envelopes on the distributional responses of tree species to climate change in dry portions of the United States. We quantified climate envelopes for six coniferous tree species and two life stages (trees and seedlings) to identify differences in distributions of forest tree species in relation to climate. Our overall objective was to determine if differences in predicted occurrence probabilities and climate envelopes suggested species range contractions, expansions or shifts. We answered the following questions: (1) Does the probability of tree occurrence differ from the probability of seedling occurrence, and which regions experience the greatest differences? (2) Does the breadth of temperature and precipitation envelopes differ among species or between life stages? (3) Are seedling climate envelope boundaries different from tree boundaries and what does this suggest about distributional changes? We quantified the impacts of spatial variation in temperature and precipitation regimes on the occurrences of tree

species across the dry domain of the western United States, highlighting potential early indicators of change in species distribution.

METHODS

Study area and species

The dry domain of the United States (Bailey, 1995) spans landscapes from the eastern slope of the Sierra Nevada and Cascade Mountains to the central Great Plains (Fig. S1 in Supporting Information). Although we included a large portion of the present range of many western North American tree species, we did not address populations in Canada, Mexico or the Pacific Coast which account for large portions of the ranges of some species (Burns & Honkala, 1990). We excluded these areas either because forest inventory data were not easily available (i.e. Canada and Mexico) or because populations in other regions may represent other subspecies or genotypes (i.e. the Pacific Coast; Jaramillo-Correa *et al.*, 2009). However, by incorporating a large, heterogeneous area encompassing both lower and upper elevational species range margins, we assumed that we captured a broad scope of climate and ecosystem types representing much of the climatic ranges of our study species. Furthermore, by minimizing the potential for model over-fitting (see Model development), we probably improved the generality of these results with respect to other regions (Randin *et al.*, 2006).

We focused on six broadly distributed forest tree species with 1020 to 7429 observations of tree occurrence in the FIA database (see Data), with the prevalence (i.e. the proportion of plots with observed occurrences) of any given species or life stage ranging from 0.03 to 0.26 (Table 1). The study species included trees common to high-elevation subalpine forests (*Abies lasiocarpa* (Hook.) Nutt., *Picea engelmannii* Parry ex Engelm. and *Pinus albicaulis* Engelm.) and low-elevation montane forests (*Pinus contorta* Douglas ex Loudon, *Pinus ponderosa* Lawson & C.

Lawson and *Pseudotsuga menziesii* (Mirb.) Franco), which are commonly associated with well-defined climatic conditions (Peet, 1981). Because the elevational ranges of each species vary greatly across the study area due to regional variation in climate (Burns & Honkala, 1990), we defined montane tree species as those with distributions extending to the lower forest ecotones where semi-arid woodlands, shrublands and grasslands dominate and subalpine tree species as those with distributions extending to the cold, upper forest ecotones where alpine vegetation dominates.

Data

The FIA database (<http://www.fia.fs.fed.us/>) provides detailed information regarding forest composition, structure and health (Woudenberg *et al.*, 2010). FIA plot locations are distributed across the forested portion of the United States with approximately one plot per 2500 ha. We limited our analysis to forested plots with the current national standard FIA plot design inventoried once between 1999 and 2010 (28,177 forest plots). Each plot was composed of four subplots covering 168.3 m² with a 13.5 m² microplot near the centre of each subplot (a total area of 673.3 and 53.8 m², respectively). The diameter, health status and location of each tree [> 12.7 cm diameter at breast height (d.b.h.)] in the subplots was measured. Tree seedlings (< 2.54 cm d.b.h. and > 0.15 m height) were identified to species and counted in each microplot. We extracted 30-year climate normals from the 2.5 arcsec PRISM dataset (PRISM Climate Group 2010). Because error was introduced into FIA plot locations to protect the privacy of property owners (Woudenberg *et al.*, 2010), we calculated mean climate variables at a 5-km resolution. While climate conditions can vary at relatively fine spatial scales, especially in complex topography, 5-km resolution climate data characterize broad-scale climatic controls on species distributions and were assumed to be appropriate for species distribution models of the type applied here (Pearson & Dawson, 2003).

Table 1 The number of observed occurrences, species prevalence (the proportion of plots on which the species and life stage was observed; in parentheses) and the true skill statistics (TSS) for tree and seedling species distribution models indicated that species occurrence was better predicted for high-elevation tree species than low-elevation species and for trees than seedlings. TSS were calculated based on the best model (Table 3), the mean estimated parameters (Tables S1 & S2), and the 50% cross-validation sample for each species and life stage in the study area.

Species	Abbreviation	Observed occurrences (prevalence)		TSS	
		Trees	Seedlings	Trees	Seedlings
<i>Abies lasiocarpa</i>	ABLA	4534 (0.16)	4006 (0.14)	0.78	0.77
<i>Picea engelmannii</i>	PIEN	4504 (0.16)	2778 (0.10)	0.75	0.71
<i>Pinus albicaulis</i>	PIAL	1020 (0.04)	840 (0.03)	0.79	0.79
<i>Pinus contorta</i>	PICO	4543 (0.16)	2054 (0.07)	0.71	0.67
<i>Pinus ponderosa</i>	PIPO	6100 (0.22)	2172 (0.08)	0.60	0.54
<i>Pseudotsuga menziesii</i>	PSME	7429 (0.26)	3982 (0.14)	0.65	0.57

Table 2 List of covariates and symbols for models of adult and seedling occurrence for six forest tree species. Interactions are grouped: temperature by moisture interactions and seasonal interactions.

Covariate	Symbol
Main effects and quadratic terms	
Mean annual temperature (°C)	T_i, T_i^2
Summer temperature differential (°C)	S_i, S_i^2
Mean winter precipitation (m)	w_i, w_i^2
Mean summer precipitation (m)	s_i, s_i^2
Interaction terms	
(1) Temperature \times moisture	$S_i \times s_i$ $T_i \times w_i$ $S_i \times w_i$ $T_i \times s_i$
(2) Seasonal	$T_i \times S_i$ $w_i \times s_i$

Climate variables

For many tree species in the western United States, mean, seasonal and interacting effects of temperature and precipitation shape species distributions (Shafer *et al.*, 2001; Rehfeldt *et al.*, 2006; Schrag *et al.*, 2008). We focused on the influences of temperature, moisture and their interactions (Table 2). To represent both mean and seasonality in temperature and precipitation for each plot i , we used mean annual temperature (T_i , °C), the difference between mean summer (June to September) and winter (November to March) temperatures, or temperature differentials (S_i , °C), winter precipitation (November to March; w_i , m), and summer precipitation (June to September; s_i , m). These variables were chosen because they incorporate information about both mean and seasonal climatic conditions, they explained variation in species occurrence during initial data exploration and they are not highly correlated (Pearson correlation $r < 0.7$). In addition, these climate variables have changed substantially during the past 115 years across the study area, though the degree and direction of change have been highly variable and tended to indicate greater increases in temperature and decreases in precipitation in cooler climates associated with forests (Fig. 1).

Model development

Although the use of climate envelope models to predict the responses of tree species to climate change has been widely criticized (Elith & Leathwick, 2009), climate envelope modelling is well suited for examining current distributional differences between life stages, thereby elucidating recent patterns of tree regeneration that can be related to climate (Lenoir *et al.*, 2009; Zhu *et al.*, 2012; Rabasa *et al.*, 2013). Although comparing distributional differences between life stages does not identify the mechanisms underlying observed differences, it can identify where differences exist and how they may be related to climate.

Furthermore, simple models of species occurrence can be valuable for identifying the potential impact of climate change. For example, while individual trees respond to extreme events, such as droughts and spring frosts, the biogeographical patterns of species are well-captured by models assuming simple unimodal responses to temperature and precipitation (Boucher-Lalonde *et al.*, 2012). Therefore we assume that species distribution models offer a tractable method for comparing distributions of differing life stages with important implications for forest regeneration. For the construction of species distribution models, Bayesian statistical methods, which are flexible and coherently incorporate uncertainty into model predictions (Clark, 2005), provided a powerful method for predicting climate envelopes and species occurrences along complex climate gradients.

To examine the distributional responses of tree species to climate, we fitted presence and absence data for six tree species and two life stages to four climate variables using a Bayesian logistic regression approach. The Bayesian logistic regressions were implemented using the R statistical coding language (R Development Core Team, 2010). We included quadratic terms for each covariate to represent a unimodal form of the species distributions. Our climate variables are correlated with many other climate variables and therefore incorporate information regarding the length of the growing season, evaporative demand, moisture inputs and seasonality (Boucher-Lalonde *et al.*, 2012). These variables are not likely to have independent effects on species occurrence. To capture within- and between-season interactions between temperature and precipitation effects, the models included different combinations of six two-way interactions ($T_i \times w_i$, $S_i \times s_i$, $T_i \times s_i$, $S_i \times w_i$, $T_i \times S_i$, $w_i \times s_i$; Table 2). All quadratic and interaction terms were centred to reduce collinearity. Given these variables, the probabilities of occurrence for trees ($\theta_{1,i}$) and seedlings ($\theta_{2,i}$) for a given species at plot i were modelled as a Bernoulli process with a logit link function (Appendix S2). Thus, the predicted probabilities represent the occurrence responses to observed variation in the multivariate climate space.

Over-fitting species distribution models can lead to poor transferability, raising questions as to whether models represent ecological processes or spurious correlations (Randin *et al.*, 2006). To avoid over-fitting with our Bayesian logistic regression, we used predictive loss to compare models with different combinations of interaction terms by minimizing the sum of the error sum of squares (i.e. model fit) and the predictive variance (i.e. the penalty term; Gelfand & Ghosh, 1998). Thus, minimizing predictive loss identifies simpler, parsimonious models by rewarding improved model fit while penalizing complexity. All main effects and quadratic terms were included in each model. With six potential interactions, there were $2^6 = 64$ possible models for each species. Given the length of posterior parameter simulations (Appendix S2), comparing so many models was impractical. Furthermore, exploring a large model space using forward, backward or stepwise selection techniques can result in overly complex models and can produce ecologically unrealistic combinations of variables (Araújo & Guisan, 2006; Austin, 2007).

To reduce the number of potential models and focus on ecologically relevant models, we grouped interactions into temperature by precipitation and seasonal interactions (Table 2). We compared models with all main and quadratic effects (null) to models with temperature by precipitation interactions, seasonal interactions and all interactions (full). Rising mean annual temperatures will increase evaporative demand, thus reducing soil water availability if precipitation does not increase to offset losses. Temperature by precipitation interactions ($T_i \times w_i$, $S_i \times s_i$, $T_i \times s_i$ and $S_i \times w_i$) can represent the impact of temperature on how much precipitation becomes available for plant uptake. The effect of seasonality may depend upon average conditions (e.g. mean annual temperature T_i and temperature differential S_i) or precipitation inputs may not have an additive effect (e.g. winter w_i and summer s_i precipitation). Seasonal interactions ($T_i \times S_i$ and $w_i \times s_i$) account for potential amplification or dampening of temperature and precipitation effects on species occurrence by seasonality.

We further assessed model fits by calculating true skill statistics (TSS; Allouche *et al.*, 2006) for each species and life stage using out-of-sample validation. After the models were fitted to the complete dataset, we removed 50% of the data (i.e. a validation sample) and fitted the models again, using the posterior mean parameter estimates as the initial values for the adaptive Metropolis–Hastings algorithm. Mean probabilities of occurrence were predicted for the validation sample. We calculated the maximum TSS and the associated threshold probability for each life stage and species and defined the species range as all pixels with a probability of tree occurrence greater than the threshold.

Estimating climate envelope boundaries

In addition to examining patterns in the probabilities of occurrence given observed climate, we examined the influences of individual climate variables on species and life-stage climate envelope boundaries. Climate envelopes for each response variable were predicted from 2000 randomly selected realizations of the parameter estimates. We predicted the mean probability of tree and seedling occurrences with respect to a single response variable conditioned on all other climate variables equal to the mean for locations where the species was observed to be present (i.e. climate variable given species presence). These conditional predicted probabilities simplify the observed climatic complexity to allow for examination of the predicted effects of each climate variable on species and life-stage occurrence. Using the conditional predicted probabilities, we calculated the 10th and 90th percentile climate envelope boundaries based on the range of each climate variable for which 80% of the distribution of occurrence probabilities was included (Fig. 2; see also Bertrand *et al.*, 2011). We calculated the life-stage climate envelope boundary differences as the mean and 95% credible interval for the differences between seedling climate envelope boundaries and tree climate envelope boundaries for each species with respect to each climate variable. While the selection of the percentile upon which the envelope boundaries were based must,

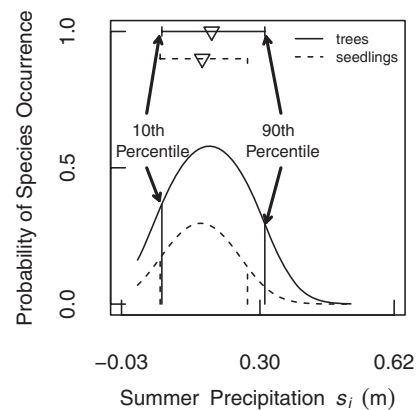


Figure 2 Probabilities of occurrence of *Pinus contorta* with respect to mean summer precipitation (s_i) are presented as an example of how climate envelopes with respect to a single climate variable, and the associated range boundaries, were calculated. Climate envelopes for trees (solid lines) and seedlings (dashed lines) were defined by the 10th and 90th percentiles with respect to a given climate variable using the area under the predicted probability curves for tree $\theta_{1,i}$ or seedling $\theta_{2,i}$ occurrence. For predictions, only the variable listed below the climate envelope was varied; all other climate variables were held constant at the mean for locations where the species was observed to be present.

by definition, influence the location and breadth of climate envelopes, differences in climate envelope boundaries between life stages were robust to a broad range of percentile values; consistent biases were not observed from 5th to 25th and 75th to 95th percentiles (Fig. S2). As opposed to a comparison of envelope differences across all species (Bertrand *et al.*, 2011), we incorporated uncertainty in our predictions to examine differences in climate envelope boundaries between life stages of individual species. Therefore, our method better incorporates uncertainty relevant to species distribution modelling (Wiens *et al.*, 2009).

We chose the above definition of climate envelope boundaries to address differences in the probability of occurrence caused by differing detection probabilities associated with variable sampling intensity. As is common in forestry and forest ecology, seedlings were censused less intensively than trees on FIA plots (53.8 m² vs. 673.3 m², respectively). While foresters and forest ecologists commonly sample seedlings on smaller areas than adult trees (Avery & Burkhart, 2002), variation in sampling intensity could potentially result in a reduced probability of detection, and thus a reduced predicted probability of occurrence. However, if the sample area and the size of individuals determine the detection probability (Kobe & Vriesendorp, 2009), then it is reasonable to assume that the detection probability may vary little among plots if the sampling design remains constant. Given that the integration of two functions (f and g) with respect to a variable x , where one function (g) does not vary with x (i.e. $\int gf(x)dx = g\int f(x)dx$), the range of values of x associated with the central 80% of the area under the curve is not affected by g . It follows that the definition of climate

Table 3 Posterior predictive loss for two life stages (trees and seedlings) and six species indicated that the best models for species occurrence included either all interactions (11 of 12) or temperature by precipitation interactions (1 of 12). See Table 1 for species abbreviations.

Species	Stage	No interactions	Temperature-precipitation interactions	Seasonal interactions	Full model
ABLA	Tree	3514	3506	3500	3495*
	Seedling	3494	3487	3481	3478*
PIEN	Tree	3772	3756	3769	3752*
	Seedling	3226	3215*	3230	3217
PIAL	Tree	1429	1412	1426	1411*
	Seedling	1220	1207	1214	1203*
PICO	Tree	4557	4476	4491	4446*
	Seedling	2820	2795	2779	2774*
PIPO	Tree	6545	6095	6383	5903*
	Seedling	3582	3470	3547	3431*
PSME	Tree	7267	6998	7133	6970*
	Seedling	5239	5171	5203	5162*

*Asterisks indicate the best model (i.e. minimum predictive loss).

envelope boundaries used here and elsewhere (Bertrand *et al.*, 2011) is robust to detection errors. We assume that the large sample sizes inherent in the FIA data and often high seedling densities in forests may preserve the functional response in spite of potential detection errors, an assumption that several recent studies have relied upon (Woodall *et al.*, 2009, 2010, 2013; Zhu *et al.*, 2012). Thus, despite potential biases in predicting the probability of species occurrence, FIA data provide valuable information regarding the responses of differing species and life stages to climate, especially when climate envelope boundaries recognize sampling design.

RESULTS

Climate envelope performance

Across species and life stages, the full model was chosen as the best model in all cases but one (temperature by precipitation interactions only for *Picea engelmannii* seedlings; Table 3). Parameter estimates are provided in Tables S1 & S2. The climate envelope models predicted species distributions well, though subalpine species were better predicted than montane species ($0.71 \leq \text{TSS} \leq 0.79$ and $0.54 \leq \text{TSS} \leq 0.71$, respectively; Table 1). The quality of fits for seedlings was generally similar to those of adult trees despite the large differences in prevalence between life stages (Table 1).

Species and life stage occurrence probabilities

Predicted probability of occurrence varied by species and life stage. Predicted seedling probabilities were lower than probabilities of tree occurrence, though the magnitude of these differences also varied by species (Figs 3, S3 & S4). The differences in the predicted probability of occurrence were greatest for *P. contorta*, *P. ponderosa* and *P. menziesii* and smallest for

A. lasiocarpa, *P. engelmannii* and *P. albicaulis*. Thus, probabilities of seedling occurrence were generally less than tree probabilities and these differences were greatest for montane species.

Though the magnitude and pattern of the differences varied by species, differences between the mean predicted probability of occurrence of seedlings and adults were nearly always negative (Figs. 4). Subalpine species (*A. lasiocarpa*, *P. engelmannii* and *Pinus albicaulis*) exhibited less extreme differences (i.e. less negative) across the majority of their ranges, while montane species (*P. contorta*, *P. ponderosa* and *P. menziesii*) exhibited differences ranging up to -100% . Extreme differences (i.e. more negative) were often observed in the western or southern portions of the ranges and near climate envelope boundaries, whereas smaller differences were observed in regions with high probability of occurrence (see Figs S3 & S4). However, some species exhibited less extreme differences between life stages near climate envelope boundaries, such as *P. albicaulis*, *P. ponderosa* and *P. menziesii* seedlings along their eastern range margins (Fig. 4).

Envelope breadth and envelope boundaries

Climate envelope location and breadth varied among species (Fig. 5). Some montane species (*P. ponderosa* and *P. menziesii*) were associated with warmer conditions than subalpine species and *P. engelmannii* and *P. ponderosa* were associated with smaller temperature differentials than the other species. Envelopes with respect to winter and summer precipitation were narrowest for *P. ponderosa* and *P. contorta*, respectively, while summer precipitation envelope breadths were broadest for *P. albicaulis* and *P. menziesii*. The minimum winter precipitation decreased from subalpine to montane tree species. As evidenced by a greater proportion of the observed variation in climatic conditions included in climate envelopes, precipitation envelopes were generally broader than temperature envelopes. Within a given species, seedlings were associated with conditions similar to adult trees, though envelope breadth varied.

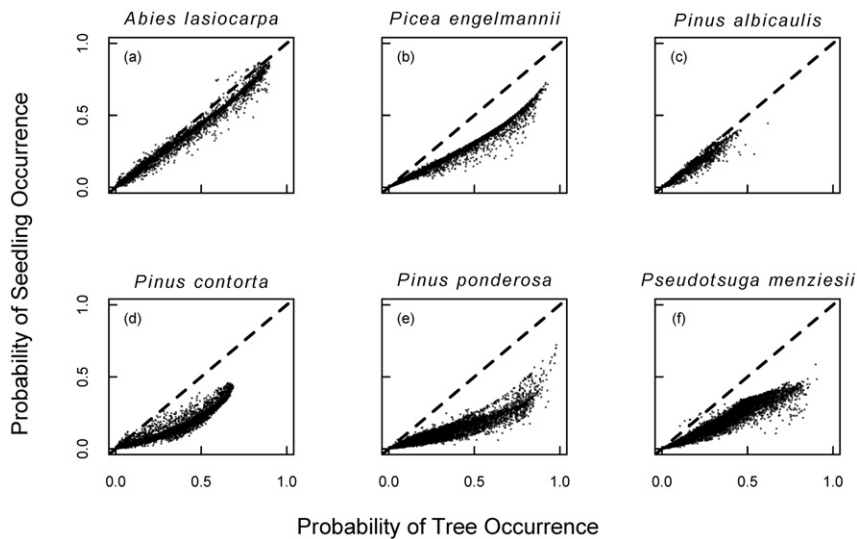


Figure 3 Compared with adult trees, seedlings were less likely to be present and this difference increased from high-elevation species (a–c) to low-elevation species (d–f), as indicated by comparisons of mean predicted probabilities of tree occurrence and seedling occurrence for (a) *A. lasiocarpa*, (b) *P. engelmannii*, (c) *P. albicaulis*, (d) *P. contorta*, (e) *P. ponderosa*, and (f) *P. menziesii*. The 1 : 1 line (i.e. no difference in occurrence probability) is represented by dashed line.

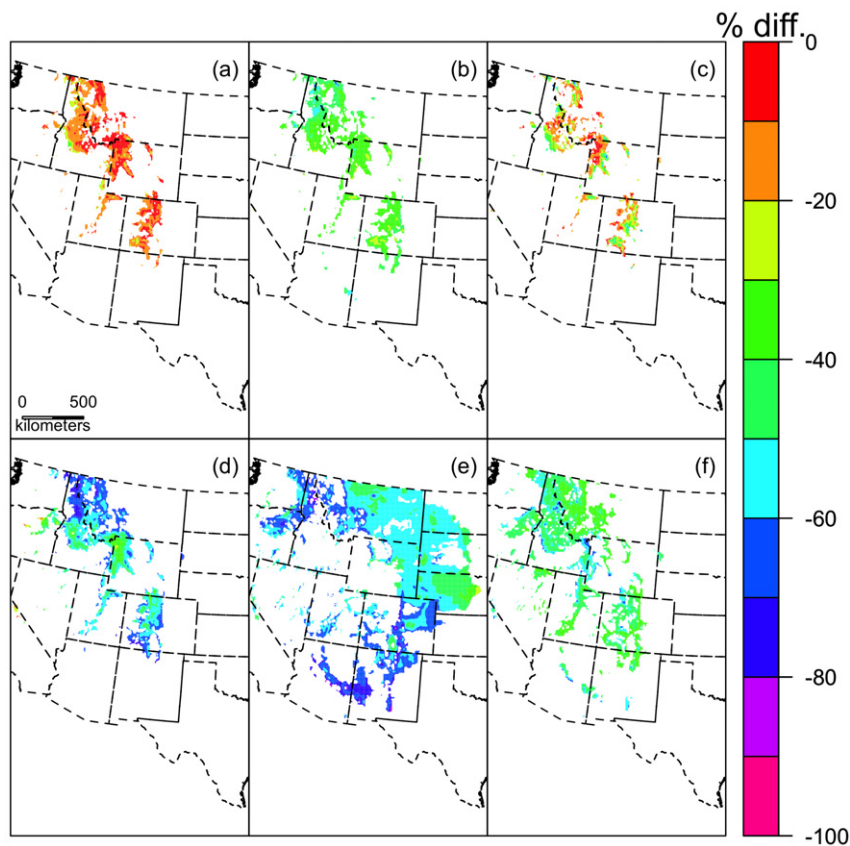


Figure 4 Geographic variation in the differences between tree and seedling distribution was examined using the percentage differences between seedling and tree mean predicted probabilities of occurrence $[(\theta_{2,i} - \theta_{1,i})/\theta_{1,i} \times 100]$ for (a) *A. lasiocarpa*, (b) *P. engelmannii*, (c) *P. albicaulis*, (d) *P. contorta*, (e) *P. ponderosa*, and (f) *P. menziesii* across the tree ranges described in Fig. S3. For example, more-negative differences (blue, purple and pink) indicate that seedlings are less likely to occur than adult trees, while less-negative differences (green, yellow and red) indicate similar probabilities of occurrence between seedlings and adults. The spatial resolution of predictions is 10 km. State boundaries are delineated by dashed lines.

The climate envelope boundaries of seedlings often differed from those of trees, especially for montane tree species (Fig. 6). For montane tree species (*P. contorta*, *P. ponderosa* and *P. menziesii*), 16 out of 24 climate envelope boundaries (three species \times four climate variables \times two boundaries) differed from zero, while only 2 out of 24 climate envelope boundaries differed from zero for subalpine species (*A. lasiocarpa*, *P. engelmannii* and *P. albicaulis*). Most climate envelope boundary differences at the 90th percentile, a measure of the maximum temperature and

precipitation values defining the envelope, were negative (nine negative versus two positive), suggesting range contractions. Differences at the 10th percentile, a measure of the minimum temperature and precipitation values defining the envelope, indicated both expansions and contractions of the climate envelope boundary, though contractions were more common (two negative and five positive, respectively). For many species, mean seedling climate envelope boundary differences were negative for winter precipitation at the 10th and 90th percentiles.

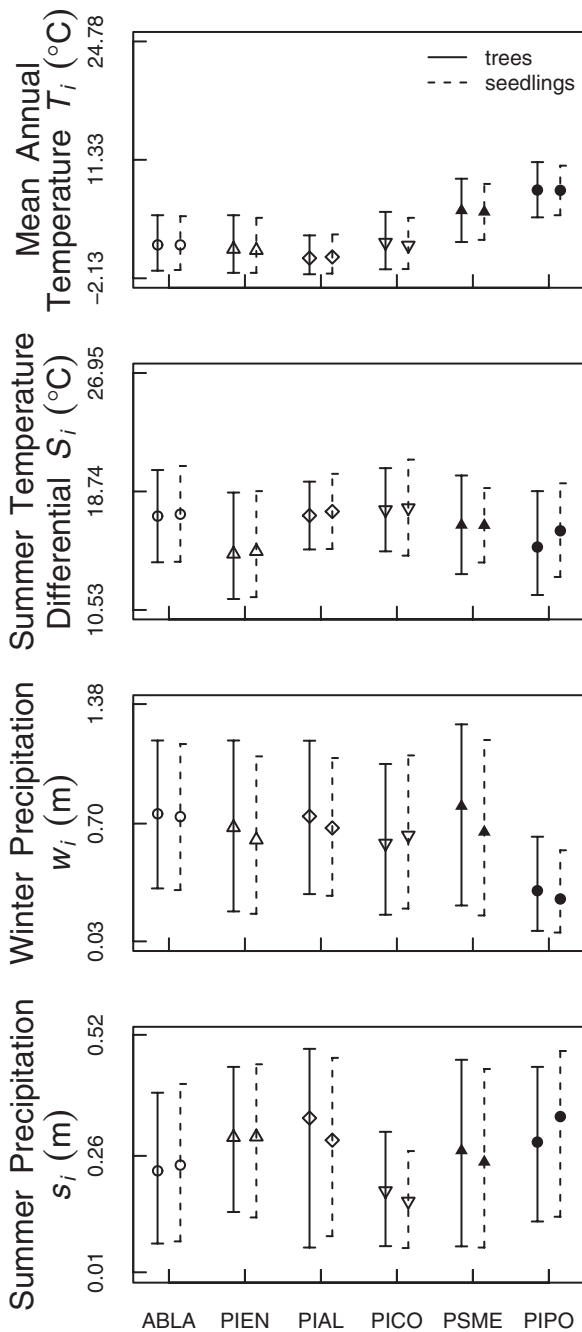


Figure 5 Climate envelopes (10th to 90th percentiles of the area under the predicted probability curves, see Fig. 2) with respect to each climate variable showed the variation in observed climate niches across species and life stages. For each species, tree (solid lines) and seedling (dashed lines) climate envelopes were presented. Species are sorted from high to low elevation. See Table 1 for species abbreviations.

DISCUSSION

Differences between life stages in the climate envelopes of forest tree species support the idea that patterns of tree regeneration are changing in response to recent climate change. For many of the species examined here, particularly montane species

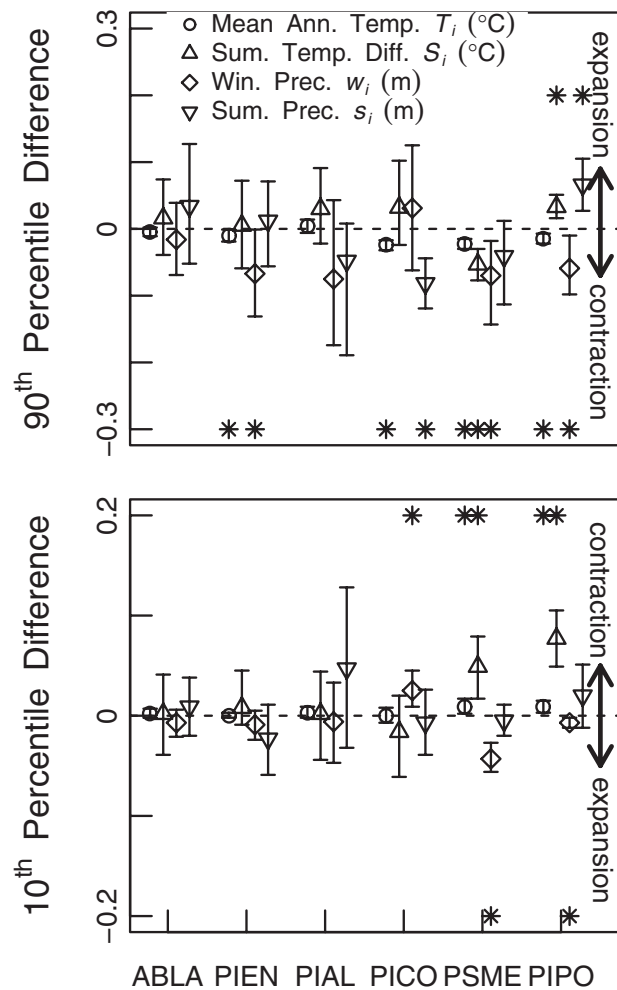


Figure 6 Mean and 95% predictive intervals for the relative differences between seedling and tree 10th and 90th percentile climate envelope boundaries for six tree species and four climate variables indicated that climate envelope contractions were more common than expansions (14 contractions versus 4 expansions), especially at higher values of the climate variables. Climate envelope differences were normalized to the range of the climate variable for the purposes of comparison. Asterisks indicate that the credible intervals do not include zero. Species are sorted from high to low elevation. See Table 1 for species abbreviations.

(*P. contorta*, *P. ponderosa* and *P. menziesii*), seedling climate envelope boundaries differed from adult trees (Fig. 6) and the relative differences in occurrence probability varied geographically (Fig. 4). Differences in climate envelope boundaries indicated that range changes are more likely for montane species than for subalpine species and that contractions and shifts appear to be the most common changes (Fig. 6, Table 4). Because previous range shifts of tree species in response to changing climates have been linked to differences between tree regeneration and adult survival niche (Jackson *et al.*, 2009) and the presence of adult trees implies that conditions were appropriate for tree regeneration in the past (Lenoir *et al.*, 2009), the

Table 4 Summary of contractions, expansions and shifts for each species and climate variable implied by envelope boundary differences (Fig. 6) indicating that differences between seedling and tree climate envelope boundaries most often imply no change, followed by contractions, shifts and expansions.

Species	Mean annual temperature	Summer temperature differential	Winter precipitation	Summer precipitation
<i>Abies lasiocarpa</i>	•	•	•	•
<i>Picea engelmannii</i>	• ↓ Contract	•	• ↓ Contract	•
<i>Pinus albicaulis</i>	•	•	•	•
<i>Pinus contorta</i>	• ↓ Contract	•	• ↓ Contract	• ↓ Contract
<i>Pinus ponderosa</i>	• ↓ Contract	• ↑ Shift	• ↑ Shift	• ↑ Expand
<i>Pseudotsuga menziesii</i>	• ↓ Contract ↑	• ↓ Contract ↑	• ↓ Shift ↓	• • • ↓

Differences between range boundaries of early life stages and climatic range boundaries of trees for the 10th and 90th percentiles (lower and upper symbols, respectively): no difference (•), positive (↑), and negative (↓) for seedling versus tree comparisons. Range contractions were defined by range boundaries contracting at both the 10th (i.e. positive difference) and 90th (i.e. negative difference) percentiles or contracting at one range boundary and no difference at the other. Range expansions were defined by range boundaries expanding at both the 10th (i.e. negative difference) and 90th (i.e. positive difference) percentiles or expanding at one range boundary and no difference at the other. Range shifts were defined as situations where both range boundary differences were positive or negative.

differences in present-day climate envelopes highlight the influences of climate on recent forest regeneration and the potential for continued range shifts.

Early indications of range shift

Species range shifts in response to climate change depend on demographic processes at range margins (Morin *et al.*, 2007; Thuiller *et al.*, 2008), but it remains unclear whether range shifts will be dominated by general biogeographic patterns, such as failure to migrate (Zhu *et al.*, 2012), upslope migration (Lenoir *et al.*, 2009; Vitasse *et al.*, 2012) or even transient downslope migrations associated with biotic interactions (Lenoir *et al.*, 2010). We found support for range margin shifts into cooler habitats consistent with upslope migration, but we found nearly four times as many examples of climate envelope boundary differences consistent with range contraction as range expansion (14 vs. 4; Fig. 6). When both boundaries were considered simultaneously, our results indicated that contraction and no change in tree species climate envelopes were the most common outcomes (33.3 and 50% of species–climate comparisons, respectively), followed by shifts (12.5%) and expansion (4.1%) (Table 4). Interestingly, 29% of these observed contractions were associated with movement away from warm climates (i.e. 4 of the 14 differences consistent with contractions were negative

differences at the 90th percentile climate envelope for mean annual temperature; Fig. 6). Given that temperature increases are the most consistent regional climate change in recent history (Fig. 1), these contractions may offer some additional support for upslope migration in the form of increasingly skewed distributions (Kelly & Goulden, 2008). These skewed distributions imply that regeneration failures along warmer climate envelope boundaries are occurring at a faster pace than potential expansions along cooler climate envelope boundaries.

Despite our observation of broad winter precipitation envelopes (Fig. 5), differences between seedling and adult climate envelope boundaries with respect to winter precipitation were often negative (5 out of 12 comparisons; Fig. 6), indicating a general shift toward drier winter conditions. This may indicate reduced establishment or survival in locations with greater snowpack, as might be expected if the timing of snowmelt limits the length of the growing season (Schlaepfer *et al.*, 2012) or if snow fungi are an important agent of mortality for immature trees (Barbeito *et al.*, 2012). Furthermore, higher winter precipitation may be of little use to tree seedlings since less-developed root systems limit their ability to reach deeper soil layers (Cavender-Bares & Bazzaz, 2000) where substantial water from snowmelt can be stored (Williams *et al.*, 2009).

Simple generalizations did not fully represent climate-induced range shifts of these tree species. Climate envelope

boundary differences between life stages for individual species may indicate range shift, contraction, expansion or no change in relation to a specific climate variable (Table 4), despite the overall trend toward individual climate envelope boundary contractions (Fig. 6). Such interspecific variation implies that there will be both winners and losers under climate change and that studies need to examine diverse suites of species in order to predict future ecosystem change (Dawson *et al.*, 2011). These patterns validate our approach by highlighting the importance of examining the distributional responses of species across a broad range of climates incorporating both lower and upper climate envelope boundaries.

Differences in tree occurrence between life stages

The observed differences in species occurrence between life stages offers interesting evidence of species responses to climate, though FIA sample design may also play a role. Given the sensitivity of range boundaries to climate, increasing differences in the probability of occurrence between differing life stages suggests that climate change has already caused a shift in regeneration potential in some areas. Differences in the predicted probability of occurrence of trees versus seedlings (Fig. 3) provided evidence of gradients in tree regeneration, such as increasing differences in probabilities of occurrence of seedlings versus trees from eastern to western ranges in subalpine species (Fig. 4). Unexpectedly, our results indicated that regeneration failures were pronounced in the northern portion of study area for *P. engelmannii*, *P. contorta* and *P. ponderosa*. Although these are often considered part of the core range for some of our study species (Burns & Honkala, 1990), these areas have experienced substantial changes in climate during the 20th century (Westerling, 2006). This suggests that populations at risk of reproductive failure include not only those along southern and western range margins but can also include those in core areas.

Because differences between life stages in probabilities of occurrence indicated that habitats near the climatic optimum (i.e. with the highest probability of occurrence; Figs S3 & S4) for a species provided more opportunities for successful regeneration (i.e. smaller percentage differences in probability of occurrence; Fig. 4), increasingly episodic regeneration in marginal versus core populations could explain the observed differences in species occurrence. Alternatively, since shade tolerance in forest trees of western North America declines from high- to low-elevation species (Haugo *et al.*, 2010), the increasing magnitude of these differences in probability of occurrence could be related to shading of seedlings by adults. The episodic nature of tree regeneration in water-limited ecosystems results from variation in tree fecundity and the competitive environment caused by climate or disturbance (Brown & Wu, 2005). If these sources of variation result in patchy distributions of seedlings, episodic and spatially variable regeneration may have led to low probabilities of occurrence for early tree life stages compared with adults.

Alternatively, bias may be introduced by variation in sampling intensity between life stages, resulting in the observed differ-

ences. Occurrence probabilities for seedlings were generally lower than for adult trees (Figs. 3). However, seedling models performed similarly to models for adults (Table 1). The combination of large sample sizes (Zhu *et al.*, 2012) and the method of calculating climate envelope boundaries (Bertrand *et al.*, 2011) lends robustness to our conclusions based on climate envelope boundaries (Figs 5 & 6), but how might relative differences between probabilities of seedling and tree occurrence (Fig. 4) be affected by sampling intensity? Detection errors, if they are prevalent in these data, are unlikely to vary systematically in climatic or geographic space. Instead, detection errors depend on the size of individuals (seedlings versus trees, in this case) and the size of the plots used to study them (Kobe & Vriesendorp, 2009). Given that the sample design remained constant across the study area, detection errors are unlikely to play a major role in the geographic patterns of the differences examined in this study. Furthermore, the magnitudes of the differences between seedlings and adults were small for some species (*A. lasiocarpa* and *P. albicaulis*; Fig. 3), indicating that differences are more likely to be a result of species biology and life history, such as the prevalence of episodic regeneration.

Limitations on inference

Our research examines variation between occurrence probabilities for different life stages as an early indication of range expansion, but both the FIA data and the modelling approach have important limitations. First, because our analysis did not utilize repeated measurements of FIA plots, these results cannot directly assess changes associated with climate change. However, the differences between life stages in the observed biogeographical patterns have been associated with past species expansion or contraction (Jackson *et al.*, 2009). Given that western conifers can survive for centuries, forest inventories may not be capable of disentangling these dynamics, but studies of the differences in current biogeography can elucidate general patterns.

Second, the lack of or exclusion of data associated with other regions of North America (i.e. Mexico, Canada and the Pacific Coast) or non-forested areas (Fig. S1) could lead to bias in the climate space being represented. However, our analysis is probably robust to these regional issues because our TSS scores were high for the 50% validation sample, indicating generality (Table 1), and our study contains the species elevational ranges, from lower forest ecotones adjacent to shrublands and grasslands to upper forest ecotones adjacent to alpine meadows (Burns & Honkala, 1990). In addition, our selection of only four climate variables and the simple logistic model results in greater transferability to, and thus representativeness of, other regions (Randin *et al.*, 2006; Boucher-Lalonde *et al.*, 2012). While biogeographic studies should endeavour to include as much information about the species of interest as possible, it is unlikely that our results were substantially biased in this case.

Lastly, simplifying climatic effects and excluding biotic interactions from our analysis limits the interpretation of our results. Temperature and precipitation surely affect water availability, but fine-scale factors, such as soils, topography and vegetation,

mediate climatic effects on soil water balance: climatic data are a proxy for the conditions experienced by plants. However, temperature and precipitation are often sufficient to capture broad patterns in tree species distributions without explicitly accounting for fine-scale ecological processes (Pearson & Dawson, 2003; Boucher-Lalonde *et al.*, 2012). In addition, shading may mediate the responses of trees to climate (Clark *et al.*, 2012), resulting in potentially misleading predictions of future species ranges derived from species distribution modelling (Clark *et al.*, 2011). The availability of light in the understorey has long been identified as a dominant control on tree regeneration (Watt, 1947), implying that disturbance could play an important role in determining the regeneration patterns of tree species, especially along range margins.

CONCLUSIONS

There is abundant evidence that important climatic controls on the distributions of tree species have changed over the past half-century (MacDonald, 2010; Seager & Vecchi, 2010). Even though the regeneration niche is expected to differ from the adult survival niche (Grubb, 1977), the climate envelope differences we observed between life stages suggest that tree populations are responding to these changes. Our results demonstrate potential range contractions and shifts with respect to temperature and precipitation conditions. The lack of consistent distributional shifts for all species emphasizes the importance of studying diverse suites of species. Climate change threatens the survival of adult trees in many forests of the western United States (Breshears *et al.*, 2005; van Mantgem *et al.*, 2009; Ma *et al.*, 2012), but even if this were not the case, tree species ranges would eventually contract if regeneration fails. These range shifts may lead to changes in forest type and/or expansion of grassland and shrubland ecosystems at lower elevational range boundaries and loss of alpine ecosystems at upper boundaries, with potentially important consequences for ecosystem functioning, such as carbon and water cycling.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Maps of the geographic distribution of Forest Inventory and Analysis plots.

Appendix S2 Bayesian model development and fitting.

Appendix S3 Sensitivity of climate envelope differences to choice of percentile.

Appendix S4 Estimated model parameters and standard deviations.

Appendix S5 Additional maps of predicted probabilities of occurrence.

BIOSKETCH

The authors' research collaboration aims to understand the consequences of climate change for plant communities, especially those that are water limited. In particular, they are interested in climatic and hydrological controls on tree regeneration in the western United States and what they imply about future forest composition and structure.

Author contributions: D.M.B., J.B.B. and W.K.L. developed the ideas and interpreted the results. D.M.B. analysed the data and led the writing.

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