

Mountain landscapes offer few opportunities for high-elevation tree species migration

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Abstract

Climate change is anticipated to alter plant species distributions. Regional context, notably the spatial complexity of climatic gradients, may influence species migration potential. While high-elevation species may benefit from steep climate gradients in mountain regions, their persistence may be threatened by limited suitable habitat as land area decreases with elevation. To untangle these apparently contradictory predictions for mountainous regions, we evaluated the climatic suitability of four coniferous forest tree species of the western United States based on species distribution modeling (SDM) and examined changes in climatically suitable areas under predicted climate change. We used forest structural information relating to tree species dominance, productivity, and demography from an extensive forest inventory system to assess the strength of inferences made with a SDM approach. We found that tree species dominance, productivity, and recruitment were highest where climatic suitability (i.e., probability of species occurrence under certain climate conditions) was high, supporting the use of predicted climatic suitability in examining species risk to climate change. By predicting changes in climatic suitability over the next century, we found that climatic suitability will likely decline, both in areas currently occupied by each tree species and in nearby unoccupied areas to which species might migrate in the future. These trends were most dramatic for high elevation species. Climatic changes predicted over the next century will dramatically reduce climatically suitable areas for high-elevation tree species while a lower elevation species, *Pinus ponderosa*, will be well positioned to shift upslope across the region. Reductions in suitable area for high-elevation species imply that even unlimited migration would be insufficient to offset predicted habitat loss, underscoring the vulnerability of these high-elevation species to climatic changes.

Keywords: climate change, demography, dominance, forest inventory and analysis, productivity, suitability, tree species, upslope migration

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Introduction

Climate change is predicted to alter the distribution of tree species and forests across the Earth (Davis & Shaw, 2001; Hansen *et al.*, 2001; Shafer *et al.*, 2001; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Iverson *et al.*, 2008; Allen *et al.*, 2010), with these changes depending on regional context, such as climatic complexity arising from mountain regions. Mountainous regions may offer opportunities for migration in response to climate change because their topographic, and thus climatic, complexity will provide access to future suitable habitat at shorter geographic distances compared with flat regions (Loarie *et al.*, 2009; Dobrowski *et al.*, 2012). However, these opportunities may be limited for high elevation, subalpine tree species that have relatively small areas of suitable habitat available for upslope migration (Lenihan *et al.*, 2008; Macias-Fauria & Johnson, 2013). Due to the potential opportunities and

obstacles provided by mountainous regions, the effects of climatically driven changes in species persistence and migration on future tree species distributions in mountainous regions are especially uncertain.

While the ecological processes driving species distributional change operate locally (individual scale to stand scales), the resulting biogeography is observed regionally. Distributional changes are likely to be driven by demographic responses to climate change, such as increased mortality leading to reduced persistence and/or altered recruitment dynamics constraining species migration (Morin *et al.*, 2007; Thuiller *et al.*, 2008). Recent forest mortality events (Van Mantgem *et al.*, 2009; Allen *et al.*, 2010; Ma *et al.*, 2012) and shifting patterns of tree recruitment (Vitasse *et al.*, 2012; Zhu *et al.*, 2012; Bell *et al.*, 2014) may indicate that tree species demographic responses to climate change have already begun. By relating the geographic distributions of species to the environmental conditions those species experience, species distribution modeling (SDM) offers a method to examine potential distributional responses to climate change at regional scales.

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Species distribution modeling approaches attempt to infer fundamental niches (i.e., where a species can live) from occurrence data describing realized niches (i.e., where a species is observed to live) (Guisan & Zimmermann, 2000). SDM often relies on the correlation between contemporary species distributions and climate to infer climatic suitability and distributional responses to future climate change without incorporating the dynamic responses of individuals, populations, or communities, which limits the reliability and utility of predictions of distributional change (Ibáñez *et al.*, 2006; Elith & Leathwick, 2009; Clark *et al.*, 2011). Therefore, probabilities of species occurrence estimated by SDM may be suspect until they are related to other measures species performance.

The probability of species occurrence with respect to climate based on SDM approaches (hereafter referred to as climatic suitability) synthesizes the aspects of the multivariate climate space relevant to the distribution of a given species into a single variable. Climatic suitability may be more generalizable if it is related to other measures of suitability (Van Couwenberghe *et al.*, 2012). For example, increasing climatic suitability would not only be associated with increasing probability of species occurrence, but increasing species dominance, productivity, or improved demography, such as high regeneration and low mortality (Dolanc *et al.*, 2012). Forest structural metrics characterizing species dominance, productivity, regeneration, and mortality can be compared with SDM results for tree species to explore the ecological significance of climatic suitabilities, thus increasing our confidence in model predictions.

Using individual tree data from the US Forest Service Forest Inventory and Analysis (FIA) database (<http://fia.fs.fed.us>), we assessed the ecological significance of climatic suitability and the implications for response to climate change of four widespread tree species in western North America: *Abies lasiocarpa* (Hook.) Nutt., *Picea engelmannii* Parry ex Engelm., *Pinus contorta* Douglas ex Loudon, and *Pinus ponderosa* Lawson & C. Lawson. First, we assessed the ecological significance of the SDM-derived climatic suitability by examining the relationship between climatic suitability and measures of species dominance, productivity, and demography on FIA plots. Second, acknowledging the limitations of the SDM approach, we examined predicted changes in climatic suitability of (i) established tree populations as a measure of the potential impact on species persistence (i.e., no migration); and (ii) currently unoccupied landscapes, as a measure of the potential for migration. By comparing climatic suitabilities derived from SDM with relevant measures of species dominance, productivity, and demography, we assessed the ecological significance of the climatic suitabilities, an important step in

evaluating the usefulness of SDM output in examining tree species responses to global change. This assessment provides improved insight into the potential limitations imposed by migration capacity on responses of these tree species to climate change. While we share others' skepticism of range shift SDM predictions (e.g., Morin *et al.*, 2007; Morin & Thuiller, 2009), we propose that, much as studies of climate velocities provide insight into the magnitude of climate change populations will experience (Loarie *et al.*, 2009), examining future changes in climatic suitability for contemporary populations allows for the assessment of the potential risks faced by tree species. Other global change factors, such as rising CO₂, land-use change, and invasive species, are likely to mediate ecological responses to climate change but are beyond the scope of this research.

Materials and methods

This study utilized FIA data from the dry domain of the western United States, ranging from the eastern slopes of the Sierra Nevada and Cascade Mountains to the western portion of the Great Plains (Figure S1; Bailey, 1995). This region includes diverse climate regimes dominated by a variety of vegetation types, ranging from deserts to forests to alpine meadows (Peet, 1981). Western North American forests transition from relatively open forest stands (e.g., *P. ponderosa* forests) to closed canopy forests, including dense, monospecific forest stands of *P. contorta* and heterogeneous, subalpine forest stands of *A. lasiocarpa* and *P. engelmannii*, as elevation increases (Allen & Peet, 1990). We selected four study species (*A. lasiocarpa*, *P. engelmannii*, *P. contorta*, and *P. ponderosa*) because each species represents an important component of widespread forest types in western North America, each was present on greater than 4000 FIA plots within the study region (Table S1), and large portions of the species' distributional ranges were included in the study region (Burns & Honkala, 1990).

Across the study region, 28 116 forested FIA plots measured between 1999 and 2010 provided detailed information, including tree species and diameters of both live and dead trees (Woudenberg *et al.*, 2010). There is one FIA plot per 2500 ha, with individual tree measurements occurring only on forested plots (>10% tree cover). For each forested plot, individual trees greater than 12.7 cm diameter at breast height were measured for species, diameter, and status (live vs. dead) on 673.3 m². In addition, tree seedlings (<2.54 cm diameter and >0.15 m height) were censused on microplots covering 53.8 m². Currently, many FIA plots in the western United States have not been remeasured, meaning that information from these plots provides a snapshot of forest conditions. While changes in state variables provide richer inference, the size of the data set provides substantial statistical power for quantifying relationships between climate and tree species occurrence. Data analysis consisted of (i) prediction of climatic suitability (i.e., probability of species occurrence) under current climate; (ii) predicting future climatic suitability based on climate change scenarios; and (iii) the examination of the

variation in forest structure with climatic suitability. All analyses were executed with the R statistical programming language (R Development Core Team, 2010).

Climate data

Climate data were acquired from the PRISM 4-km average monthly temperature and precipitation data for 1981 to 2010 (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>), extracted at 5 km resolution to match the approximate area represented by individual FIA plots. We used 5 km resolution climate data because (i) FIA plot locations were generalized (reported location within 1 km of true location) to protect property owner privacy (Woudenberg *et al.*, 2010); (ii) coarse-scale climate data can characterize broadscale climatic controls (Pearson & Dawson, 2003; Ashcroft, 2010); (iii) most climate projections have relatively coarse resolution (e.g., 1/8 degree resolution of Maurer *et al.*, 2007); and (iv) downscaling climate projections can introduce substantial errors in climate data and resulting ecological model predictions (Bucklin *et al.*, 2012; Bishop & Beier, 2013). The coarse resolution of the climate data may represent broad patterns well, but they may also fail to identify microrefugia created by topographic effects on exposure and hydrology (Ashcroft, 2010; Austin & Van Niel, 2011; Lenoir *et al.*, 2013). Climatic microrefugia may be capable of altering landscape and regional patterns of persistence under climate change if, for example, trees can successfully recruit outside of the microrefugia. This pattern requires that tree regeneration niches be broader than adult survival niches. However, comparisons of tree adult and seedling distributions indicate narrower tree regeneration niches compared with survival niches (Lenoir *et al.*, 2009; Zhu *et al.*, 2012; Bell *et al.*, 2014), though temporal variability may still offer some opportunities (Jackson *et al.*, 2009).

Given that our study species are broadly distributed and dominate the landscapes where they are found, the presence of microrefugia is not likely to substantially buffer entire landscapes against dramatic changes in climatic suitability. Therefore, the current study's focus on broad, landscape patterns in climate could limit the reliability of predictions. While it was not our focus, it is important to note that the lack of nonclimatic factors limits the realism of predictions if those factors are also changing and if they impact species responses to climate, such as complicated feedbacks associated with elevated CO₂, temperature, and tree nutrition (Lukac *et al.*, 2010), or shifting fire regimes (Westerling *et al.*, 2006).

Probability of occurrence and climatic suitability classification

Mean and seasonal variation in temperature and precipitation control tree species distributions in western North America (Shafer *et al.*, 2001; Rehfeldt *et al.*, 2006; Schrag *et al.*, 2008), and simple models representing climatic variation in probability of species occurrence are broadly generalizable (Randin *et al.*, 2006; Boucher-Lalonde *et al.*, 2012). The current analysis is based on previously published results from an analysis of

tree distributions in the western United States that examined variation in the probability of species occurrence (i.e., climatic suitability) in response to spatial variation in mean annual temperature, the mean difference between summer (May to September) and winter (November to March) temperatures, mean winter precipitation, and mean summer precipitation (Bell *et al.*, 2014). The selected climate variables were chosen because (i) preliminary data exploration indicated these variables captured variation in tree species distributions; (ii) values of these climate variables have shifted over the last 115 years in the study region; and (iii) they were not highly correlated ($| \text{Pearson correlation} | < 0.7$), reducing issues with collinearity (Bell *et al.*, 2014).

The climatic suitability of each FIA plot was quantified by estimating the probabilities of species occurrence with respect to climate using a Bayesian logistic regression framework (Appendix S1; see also Bell *et al.*, 2014). Logistic regressions, a subset of generalized linear models, quantify the relationship between some group of predictor variables (e.g., climate) and a binomial response variable (e.g., presence and absence) and have been widely used in the modeling of species occurrence (Elith & Leathwick, 2009). Bayesian methods offer a flexible method for model fitting, selection, and prediction (Clark, 2005, 2007). Our previous work showed that four climate variables (mean annual temperature, mean difference between summer and winter temperature, mean winter precipitation, and mean summer precipitation), along with quadratic and interaction terms, explained tree species distribution well, with true skill statistics from a 50% cross-validation ranging from 0.60 to 0.78 (Bell *et al.*, 2014). These models were found to be parsimonious solutions based on posterior predictive loss, a model comparison method suited for Bayesian model output that rewards model fit and penalizes over-fitting (Gelfand & Ghosh, 1998). For the current analysis, we used the same models with the associated parameter estimates to predict current and future climatic suitabilities for FIA plots in the region (Appendix S1).

Predicting future climatic suitability

To quantify the conditions defining climatic suitability, and the consequences of projected climate change on the distribution of climatic suitability in western landscapes, we examined climatic suitability of FIA plots with respect to future climates. Specifically, we examined how climatic suitability would shift under expected climate change scenarios. We calculated predicted future climatic suitabilities based on our models for contemporary distributions (Bell *et al.*, 2014) but used three projected ensemble climate scenarios for 2070 to 2099 in the western United States (climatewizard.org; Maurer *et al.*, 2007) representing a range of severities of climate change (predicted temperature change under B1 scenario < change under A1B scenario < change under A2 scenario) (Christensen *et al.*, 2007). Therefore, future predictions of climatic suitability relied on both the parameter estimates from the species occurrence modeling (Bell *et al.*, 2014) and 1/8th-degree downscaled ensemble median temperature and precipitation predictions for 2070 to 2099 derived from 16 global circulation models for

A1B, A2, and B1 climate change scenarios (Maurer *et al.*, 2007). Scenario A1B represents an economically heterogeneous future with a balance between fossil and nonfossil energy production. Scenario A2 represents an economically heterogeneous future with localized economic development. Scenario B1 represents a future converging toward information and service economies and an emphasis on global solutions. Scenario A2 is predicted to result in the greatest climate change over the next century.

After extracting climate data for both forested and nonforested FIA plots ($n = 126648$), we categorized plots based on the suitability thresholds established under current conditions (Table S1; see below for further detail). Predictions of future species distributions developed using SDM approaches have been widely criticized for their lack of biologically relevant processes (Ibáñez *et al.*, 2006). However, the resulting climatic suitability estimated for individual species based on SDM approaches may be thought of as a synthetic proxy for climate, which incorporates biologically relevant and complex variation in multivariate climate space. Therefore, predicted changes in climatic suitability in the future represent measures of biologically important climate changes, not realized distributions of species in the future.

In this analysis, we were interested in both forested and nonforested plots because future conditions may allow trees to move beyond contemporary upper or lower forest boundaries. Future climatic suitabilities were predicted for both forested and nonforested plots, while contemporary suitabilities were predicted for forested plots only. This difference in sample size arises from the fact that we can observe whether a plot is currently forested but do not have information regarding whether it will be forested in the future. Therefore, comparisons of contemporary and future climatic suitabilities will tend to overestimate increases in the area of climatically suitable habitat (e.g., Table 1), while measures of proportional changes rather than absolute probability changes should be more robust.

Variation in forest structure with climatic suitabilities

To simplify some comparisons, climatic suitabilities were used to classify FIA plots into categories. Plots outside the climate

envelope had probabilities less than the threshold probability that maximized the true skill statistic (Table S1; Allouche *et al.*, 2006), as discussed in our previous work (Bell *et al.*, 2014). Within the climate envelopes, we partitioned plots into three groups of equal size based on the climatic suitabilities: high, intermediate, and low suitability (Figure S1). High suitability plots were defined as those with a probability of occurrence ≥ 66 th percentile probability, intermediate suitability plots were those with 33rd percentile probability \leq probability of occurrence < 66 th percentile probability, and low suitability plots were those with a probability of occurrence < 33 rd percentile probability. These thresholds (33rd and 66th percentile probabilities) (Table S1) separated plots into groups of roughly equal sizes based on probabilities of occurrence. Given the debate concerning the utility of climate envelopes (Ibáñez *et al.*, 2006), we use these categories only as a means of simplifying the presentation of results where appropriate.

After classifying high, intermediate, and low suitability plots, as well as plots outside the climate envelopes, based on the climatic suitabilities (Figure S1), we assessed the ecological significance of SDM-derived climatic suitabilities. To understand the ecological significance of climatic suitabilities, we examined the relationship of climatic suitability of FIA plots with species dominance, productivity, and demography using four forest structural characteristics for each species: relative basal area, basal area increment, seedling density, and mortality index. Relative basal area (i.e., the proportion of stand basal area comprised by a species of interest) indicated the dominance of the species within the forest community. Tree species basal area increment [i.e., (basal area) \times (stand age⁻¹)] provided a measure of forest productivity integrated over the life of the forest stand. Seedling density provided a proxy for tree regeneration at the forest stand level. Mortality index, defined as the proportion of a species' total basal area composed of dead trees, was a proxy for tree mortality.

For FIA plots with no recent record of disturbance ($n = 25\,805$), we calculated the basal area increment ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$), relative basal area, seedling density (ha^{-1}), and mortality index for the four study species. The measures of forest structure used in this work vary greatly for a variety

Table 1 Climate changes under the A2 scenario may lead to dramatic reductions in climatically high, intermediate, and low suitability areas (10^3 km^2) available for three high elevation species (*A. lasiocarpa*, *P. engelmannii*, and *P. contorta*) while these areas increased in size for the low-elevation species (*P. ponderosa*). We report the areas for suitability classes inside the predicted climate envelopes for current climate conditions and future climate conditions based on the A2 scenario and 5 km probabilities of occurrence. Percent change in suitable climates (i.e., relative change of the area inside climate envelopes from current to future conditions) under the no migration and unlimited migration scenarios were based on predicted changes for contemporary populations and for the entire study area, respectively. Because we present contemporary results for forested areas only and future results for all areas, predicted losses of suitable area are conservative

	Current Climatic Suitability Area (10^3 km^2 ; forested areas)				Future Climatic Suitability Area (10^3 km^2 ; all areas)				Percent Change (%)	
	High	Inter.	Low	Outside	High	Inter.	Low	Outside	No migr.	Unlim.migr.
<i>A.lasiocarpa</i>	43.4	55.3	66.5	480.0	2.2	13.8	43.7	4076.1	-73	-64
<i>P.engelmannii</i>	45.0	59.9	98.9	441.0	6.7	26.9	109.5	3992.7	-44	-30
<i>P.contorta</i>	56.0	69.7	107.5	411.9	0.1	5.1	75.7	4054.9	-74	-65
<i>P.ponderosa</i>	64.8	88.6	69.1	422.6	344.3	155.5	94.1	3541.9	-38	+167

of reasons, including successional history, disturbance, management, and hydrology, but we were interested in how these characteristics varied, on average, with the climatic suitabilities estimated by our statistical models. Our goal was not to understand all the factors influencing individual plot forest structure, but rather compare mean structure across climatic suitability classes. Means and 95% confidence ellipses were estimated using nonparametric bootstrapping. To facilitate comparisons among species, we log-transformed the data.

Results

Our assessment of the ecological significance of SDM-derived climatic suitabilities compared forest structural characteristics among climatic suitability categories for each species. First, we summarized the differences in climate conditions between climatic suitability classes by calculating the 95% quantiles for the bootstrapped means (i.e., confidence intervals) and the observations for mean annual temperature and precipitation. Climatic suitability decreased with mean annual temperature and, to a lesser extent, increased with mean annual precipitation for three species (*A. lasiocarpa*, *P. engelmannii*, and *P. contorta*) (Fig. 1).

Next, we summarized differences in relative basal area, basal area increment, seedling density, and mortality index for each species and climatic suitability class to examine trends in ecologically relevant measures of species dominance, productivity, and demography. For all species, basal area increment, relative basal area, and seedling density increased with climatic suitability (Fig. 2). By contrast, mean mortality index was not consistently related to climatic suitability, though we observed a trend toward increasing mortality index with increasing climatic suitability for some species (Fig. 2b).

Predicted changes in climatic suitability for contemporary tree populations are important for species persistence in response to climate change (e.g., IPCC scenarios A1B, A2, and B1), providing insight into potential future distributions in the absence of migration. Given that species migration allows species to offset habitat losses by invading new habitats, examining future tree species responses without migration represents a worst-case scenario. For all four species, climatic suitability at locations with established populations was usually predicted to decline in response to future climate, with widespread and substantial declines for the higher elevation species. Each of the three climate scenarios exhibited similar changes in plot suitability, though the magnitudes of change were smaller for A1B and B1 scenarios compared with A2 (Fig. 3; Figures S2–S4). The majority of plots shifted to a lower suitability category for high elevation species (88% for *A. lasiocarpa*

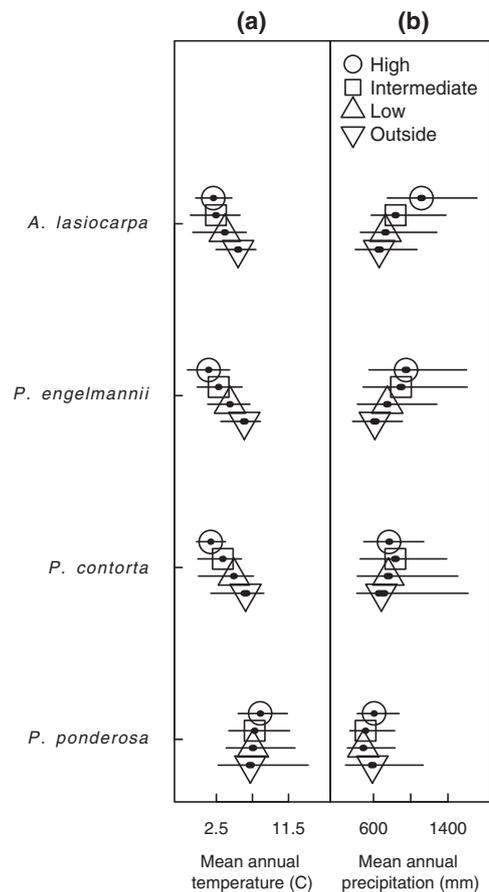


Fig. 1 Mean annual temperature (°C) and mean annual precipitation (mm) with 95% quantiles for the bootstrapped means (thick lines) and the observations (thin lines) for each species and suitability class.

pa, 87% for *P. engelmannii*, and 94% for *P. contorta*) and half of plots for the lower elevation species (50% for *P. ponderosa*) under the A2 scenario (Fig. 3a,c,e,g). High suitability plots for *A. lasiocarpa*, *P. engelmannii*, and *P. contorta* effectively disappeared and hardly declined for *P. ponderosa* (from 34% to 32% of plots).

In contrast to a future without migration, examining all locations with future suitable climates provides a best-case scenario where species are not limited by migration rates and perfectly track climate change. To assess the availability of climatically suitable areas to which species might migrate, we examined the distribution of areas of differing climatic suitability under the A2 climate scenario. Under current conditions, populations of all four species were found in close proximity (i.e., less than 200 km) to other populations of the same species (Fig. 3b,d,f,h). For all species except *P. ponderosa*, climatic suitability declined across much of the region, with higher quality climates remaining in small portions of the Rocky Mountains that represent a

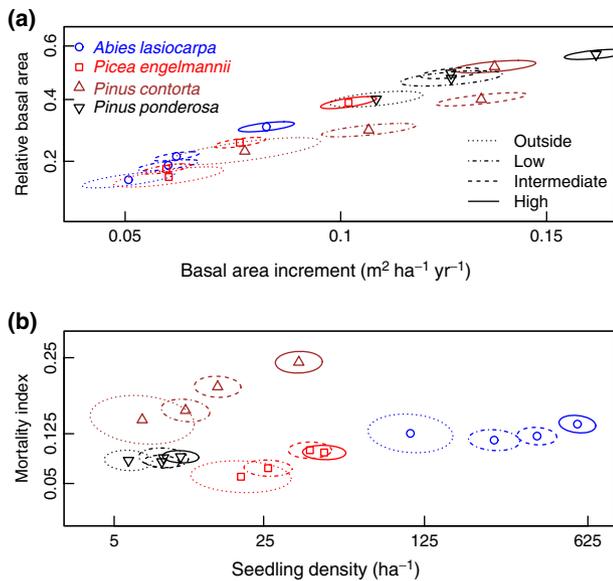


Fig. 2 Means and 95% confidence ellipses for (a) basal area increment vs. relative basal area and (b) seedling density vs. mortality index, illustrating positive trends in tree species dominance, productivity, and regeneration, but not mortality, with climatic suitability. Ellipse line styles reflect suitability level (high, intermediate, low, and outside the range) and symbols at the centers of each ellipse represent the species.

relatively small area at all distances from current populations (Figs 3 and 4).

Discussion

Our results suggest that high-elevation species will be at substantial risk under future climate change, both because they will experience dramatic declines in climatic suitability over their current range and because of the scarcity of climatically suitable areas to colonize. Tree species' biogeographic responses to climate change depend upon existing population resilience *in situ* and species' ability to migrate into nearby, climatically suitable habitats (Thuiller *et al.*, 2008; Morin & Thuiller, 2009). Interactions between the degree of climate change at a given location and the landscape or geographic context in which the location is nested could provide opportunities for migration, as might be expected in climatically complex mountain landscapes (Loarie *et al.*, 2009; Dobrowski *et al.*, 2012). The predicted risks are particularly troubling given that our comparisons of potential distributional change under future climate scenarios without migration (Figs 3, S3, and S4) and with unlimited migration (Fig. 4) represent two extremes bounding the potential responses (Meier *et al.*, 2011). In both cases, the future for high-elevation tree species in the Rocky Mountains is grim.

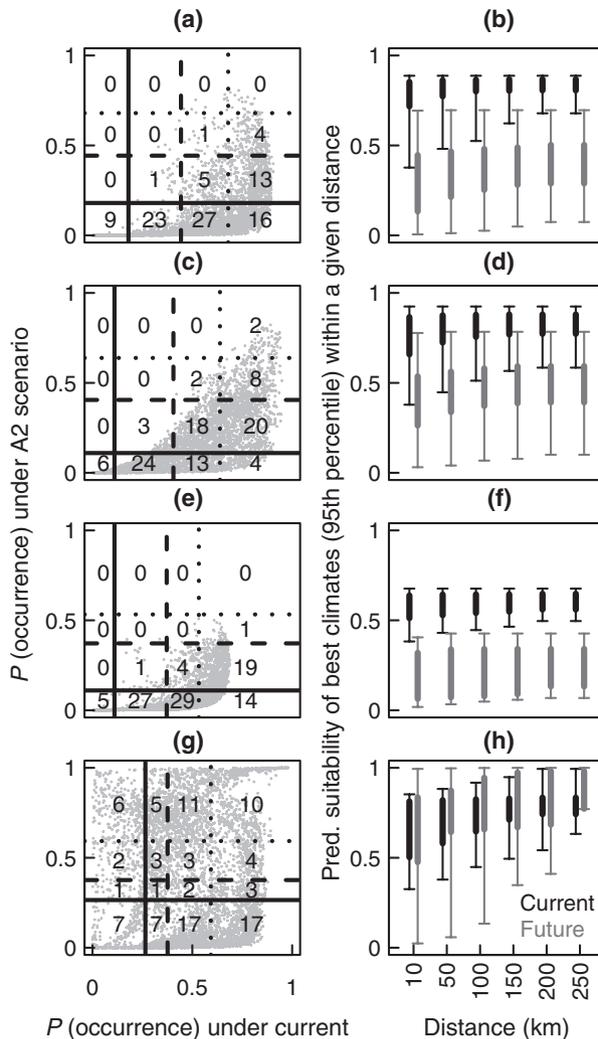


Fig. 3 For high-elevation species [*A. lasiocarpa* (a) and (b)], *P. engelmannii* (c) and (d), and *P. contorta* (e) and (f), but not the lowest elevation species [*P. ponderosa*(g) and (h)], future climate change under the A2 scenario was predicted to (a, c, e, and g) reduce climatic suitability at locations where the species are currently present (gray points) and (b, d, f, and h) decrease the climatic suitability of the best climates within certain distances (i.e., predicted 95th percentile probabilities of occurrence within a given distance). For comparisons involving locations where species are currently found (a, c, e, and g), solid lines separate low suitability plots from plots outside the climate envelope, dashed lines separate intermediate and low suitability plots, and dotted lines separate high and intermediate suitability plots (Table S1). For the examinations of the best climate at different distances (b, d, f, and h), thick lines represent 50% credible intervals and the whiskers represent 90% intervals.

Based on the climate scenarios we examined, existing tree populations are expected to experience large changes in climate, but the changes in climatic suitability varied from low to high-elevation tree species. Most of the high suitability plots for *A. lasiocarpa*,

P. engelmannii, and *P. contorta* were located in colder climates compared with *P. ponderosa* (Fig. 1). As temperatures are predicted to increase (Christensen *et al.*, 2007), much of the suitable climate space for the high-elevation species will disappear, leaving most populations in climate regimes outside their current climate envelopes (ranging from 47% to 75% of plots; Fig. 3). If these climatic conditions are associated with increasing mortality rates, recent regional forest die-off events in western North America (Breshears *et al.*, 2005; Van Mantgem *et al.*, 2009; Allen *et al.*, 2010; Ma *et al.*, 2012) are likely to continue or even accelerate. The impact and extent of forest die-offs may be further amplified by large-scale disturbances, such as wildfires. For example, dramatic increases in wildfire frequency and size associated with recent climate change and historical patterns of forest fire suppression (Westerling *et al.*, 2006) may accelerate forest change (Brown & Wu, 2005; Landhäusser *et al.*, 2010; Staver *et al.*, 2011). Alternatively, observed increases in subalpine tree regeneration could offset mortality losses, resulting in similar forest composition, but vastly different forest structure (Dolanc *et al.*, 2012).

Climatic suitabilities of landscapes within 200 km of contemporary populations also differed substantially among species. The availability of suitable climates in close proximity to contemporary populations will influence tree species migration potential. *Abies lasiocarpa*, *P. engelmannii*, and *P. contorta* are predicted to experience substantial declines in climatically suitable habitat across the region (Fig. 4). In addition, many of these high elevation areas may be geomorphically inhospitable to tree establishment (Macias-Fauria & Johnson, 2013). In contrast, *P. ponderosa* will not only have similar areas of climatically suitable habitat under future climates (Table 1), but much of this new habitat will be in close proximity to existing populations (Fig. 3h), providing widespread opportunities for migration. Similar results were found for Mediterranean plant species in Europe (Thuiller *et al.*, 2005). As tree species migration distances over the next 100 years will likely be less than 20 km (Iverson *et al.*, 2004; McLachlan *et al.*, 2005), these results suggest that high-elevation species will have few opportunities to migrate to climatically suitable nearby locations (Fig. 3b,d,f,h).

While the comparisons of changes in climatic suitabilities for currently occupied areas and the entire study region represent no migration vs. unlimited migration, respectively, they resulted in similar magnitude responses to climate change for the three high-elevation species. For example, *A. lasiocarpa*, *P. engelmannii*, and *P. contorta* experienced 44% to 74% reductions in climatically suitable plots under a no-migration scenario and 30% to 65% reductions under the unlimited migration scenario (Table 1). The small

differences for high-elevation species under the different migration scenarios support our conclusion that the high-elevation tree species are particularly vulnerable to climate change. In contrast, no migration resulted in 38% reduction in suitable plots and unlimited migration resulted in a 167% increase in area for *P. ponderosa*, indicating that understanding migration in low-elevation species will be necessary to predict future distributions (Breshears *et al.*, 2005; Van Mantgem *et al.*, 2009; Allen *et al.*, 2010; Meier *et al.*, 2011; Ma *et al.*, 2012). Therefore, while migration is an important process in tree species range shifts, it plays little role when future potential habitats are rare and/or sparsely distributed.

The current study did not explicitly examine the role of microrefugia in tree species responses to climate change. Topography will alter population exposure to climate change, allowing some populations to persist in the face of future climate change (Ashcroft, 2010; Austin & Van Niel, 2011). Microrefugia may buffer species against regional extinction by allowing them to persist locally (Randin *et al.*, 2009). Given that temporal variability in climate can offer opportunities for recruitment beyond current tree species distributions (Jackson *et al.*, 2009), populations might be able to expand, at least temporarily, into the surrounding landscapes. While these microrefugia are likely to benefit isolated populations, they are, by definition, a minor component of the landscape and their existence would not counteract widespread declines in climatically suitable areas. Therefore, declines in broadscale climatic suitability should not be interpreted as species extirpation but rather declines in the potential for landscape dominance. Furthermore, other studies have found that the use of coarser climate data in SDMs overestimates species persistence (Trivedi *et al.*, 2008; Franklin *et al.*, 2013). Thus, our predictions of climatic suitability for these high-elevation species may actually be optimistic, at least at the landscape scale.

We found that climatic suitability quantified by the SDM approach was associated with key aspects of dominance, productivity, and demography, although we observed substantial variation among species (Fig. 2). In particular, basal area increment, relative basal area, and seedling density were consistently related to climatic suitability. These results emphasize the importance of regeneration and productivity in maintaining tree dominance in response to climate. In contrast, the lack of a clear relationship between mortality index and climatic suitability (Fig. 2b) might be explained by elevational gradients in density-dependent mortality. For example, increased density-dependent mortality could be caused by increased intraspecific competition or natural enemy attack as species density and dominance increase with increasing

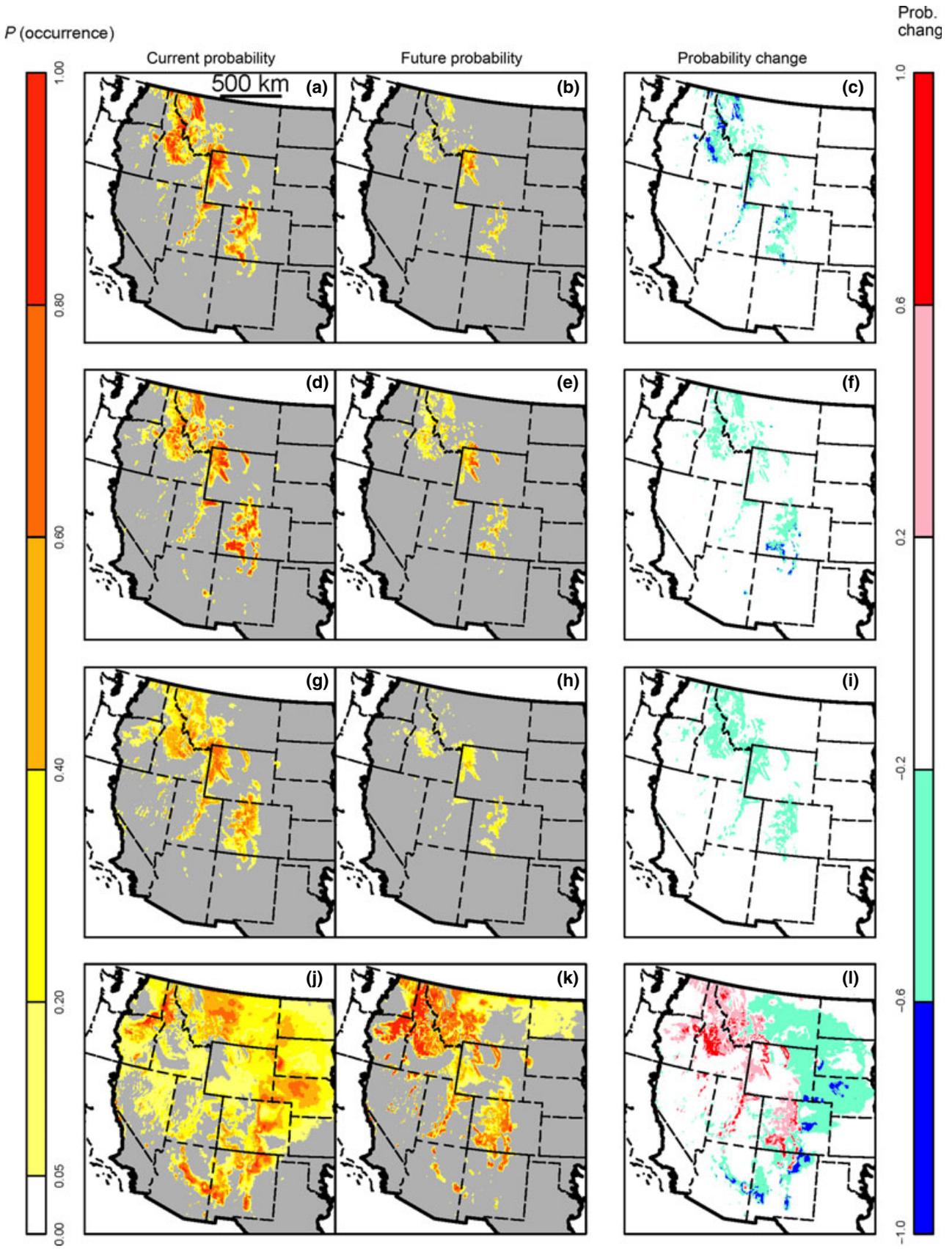


Fig. 4 The contemporary predicted probability of species occurrence (a, d, g, and j), future predicted probability of occurrence for 2070 to 2099 (A2 scenario) (b, e, h, and k), and the change in the predicted probability of occurrence (c, f, i, and l) indicate that climatic suitability is likely to decline across the region for (a–c) *A. lasiocarpa*, (d–f) *P. engelmannii*, and (g–i) *P. contorta*, whereas (j–l) *P. ponderosa* may experience declines in the southern and eastern portions of the range (i.e., American Southwest and Great Plains, respectively) and increases in the central and western portions of the range (i.e., Rocky Mountains). Results are presented at 5 km resolutions. Dashed lines indicate state boundaries and the bold line indicates the study area boundary.

climatic suitability (Fig. 2a). Alternatively, cold climates, corresponding to high suitability for *A. lasiocarpa*, *P. engelmannii*, and *P. contorta* (Fig. 1), are associated with slower rates of wood decay (Zell *et al.*, 2009; Dolanc *et al.*, 2012) and thus higher residence times for standing dead trees, potentially inflating mortality indices. Explicit integration of species demography into species distribution modeling will likely improve our understanding and predictive capabilities with regards to species and community responses to global change (Purves, 2009; Clark *et al.*, 2011; Pagel & Schurr, 2011; Vanderwel *et al.*, 2013). Regardless of the inconsistencies noted for mortality index, the observed patterns of species dominance, productivity, and regeneration support our use of SDM-derived climatic suitability in examinations of species distributional responses to climate.

Despite the potential for mountainous regions to provide opportunities for species migration (Thuiller *et al.*, 2005; Loarie *et al.*, 2009), the magnitude of climate change in the high-elevation forests examined here may be too dramatic to accommodate species persistence or dominance at a regional scale. In the western United States, if high-elevation tree species could theoretically colonize all of the upslope area currently occupied by alpine vegetation (27 621 km²) (US Geological Survey, 2011), this would offset only a small percentage of the area predicted to be lost (Table 1). The steep topography and rocky, undeveloped soils of the highest elevation areas of the Rocky Mountains will likely slow tree establishment, and thus migration, into alpine ecosystems, further limiting the availability of future habitat (Macias-Fauria & Johnson, 2013). While potential future tree and shrub range expansions have been suggested for northern populations (Shafer *et al.*, 2001), our results emphasize a threat of range contraction and local or regional declines in subalpine forests of the western United States. The magnitude of predicted climatic changes coupled with the biological significance of our measure of climatic suitability offer compelling evidence that high-elevation forests of the western United States are likely to decline in importance and may be replaced by lower elevation, drought-tolerant tree species, such as *P. ponderosa*. Given that similar patterns have been predicted elsewhere (Thuiller *et al.*, 2005; Lenihan *et al.*, 2008; Macias-Fauria & Johnson, 2013), dramatic subalpine forest declines may be likely across

the globe. However, mountain ranges with greater elevational gradients (e.g., the Himalayas) may still provide sufficient opportunities for subalpine tree species migration compared with the western United States. In addition, there is a clear need to better incorporate factors mediating climate responses, such as the complicated influences of elevated CO₂ on species responses to nutrition and climate through altered nutrient or water use efficiency (Graham *et al.*, 1990; Lukac *et al.*, 2010).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Model Specification and Fitting.

Appendix S2. Additional comparisons of contemporary and future climatic suitabilities for different species and climate change scenarios.

Figure S1. High (red), intermediate (blue), and low (gray) suitability plots for (a) *A. lasiocarpa*, (b) *P. engelmannii*, (c) *P. contorta*, and (d) *P. ponderosa* as well as plots outside the predicted climate envelope (light gray). Only plots currently occupied by the focal species were plotted. State boundaries are outlined by dashed, black lines and the study region is outlined by the bold, black line.

Figure S2. Proportion of FIA plots currently occupied by each species categorized as high (red), intermediate (blue), and low (dark gray) suitability as well as plots outside the climate envelope (light gray) for current climate compared to the future climatic suitabilities under three climate change scenarios for (a) *A. lasiocarpa*, (b) *P. engelmannii*, (c) *P. contorta*, and (d) *P. ponderosa*.

Figure S3. Implications of changing climate for abundance of suitable areas assuming no migration (i.e., persistence), presented as the probability of species occurrence for (a) *A. lasiocarpa*, (b) *P. engelmannii*, (c) *P. contorta*, and (d) *P. ponderosa* under current vs. future climate (based on scenario A1B) are presented (gray points) with the percentage of plots transitioning between each suitability category (blue indicates increases, red indicates decreases, and black indicates no change) overlaid. Solid lines separate low suitability plots from plots outside the climate envelope, the dashed lines separate intermediate and low suitability plots, and the dotted line separates high and intermediate suitability plots.

Figure S4. Implications of changing climate for abundance of suitable areas assuming no migration (i.e., persistence), presented as the probability of species occurrence for (a) *A. lasiocarpa*, (b) *P. engelmannii*, (c) *P. contorta*, and (d) *P. ponderosa* under current vs. future climate (based on scenario B1) are presented (gray points) with the percentage of plots transitioning between each suitability category (blue indicates increases, red indicates decreases, and black indicates no change) overlaid. Solid lines separate low suitability plots from plots outside the climate envelope, the dashed lines separate intermediate and low suitability plots, and the dotted line separates high and intermediate suitability plots.

Table S1. FIA plot sample size and probability of species occurrence thresholds used to define high, intermediate, and low suitability as well as outside the climate envelope (based on true skill statistics; see Methods).