**Forest structure and species traits mediate projected recruitment declines in western US tree species**

Solomon Z. Dobrowski1*, Alan K. Swanson1, John T. Abatzoglou2, Zachary A. Holden3, Hugh D. Safford4, Mike K. Schwartz5 and Daniel G. Gavin6

1Department of Forest Management, University of Montana, Missoula, MT, USA, 2Department of Geography, University of Idaho, Moscow, ID, USA, 3USDA Forest Service Region 1, Missoula, MT, USA, 4USDA Forest Service Region 5, Vallejo, CA, USA, 5USDA Forest Service Rocky Mountain Research Station, Missoula, MT, USA, 6Department of Geography, University of Oregon, Eugene, OR, USA

**ABSTRACT**

**Aim** Determine if differences in the climatic niche between conspecific adult and juvenile trees of the western Unites States vary by species traits and to assess if forest canopies moderate the sensitivity of juvenile trees to climatic variation.

**Location** The western Unites States.

**Methods** Using data from the USDA Forest Inventory and Analysis programme, we compare the distribution of conspecific adult and juvenile trees for 62 western US tree species. We relate demographic niche differences to species traits including shade and drought tolerance. We model recruitment under projected climate change using generalized linear mixed models, probabilistic uncertainty accounting, forest structural data and projected changes in the climatic water balance.

**Results** On average juveniles of western US tree species occupy a climatic subset of their conspecific adults. Demographic niche differences increase as species shade and drought tolerance increase and are greatest at climatic range margins, indicating the potential for range contractions. Models calibrated solely with climate data project recruitment declines for 2080 that are 47% larger on average than models that also account for forest structure.

**Main conclusions** Climate change-driven declines in recruitment in western US tree species may be partly offset by the moderating effect of forest canopies. The importance of this stabilizing process will depend on whether a given site is disturbed and the traits of resident species, including their ability to utilize sites that have buffered microclimates. Conversely, our results suggest that broad-scale disturbances which result in the loss of forest canopy will amplify the effects of climate change on tree recruitment.

**Keywords** Climate change, demographic niche differences, facilitation, tree regeneration, water balance, western USA.

**INTRODUCTION**

Multiple studies have forecast dramatic changes in the range and extent of western US tree species (e.g. Rehfeldt et al., 2006; Gray & Hamann, 2012). These studies rarely consider the regeneration requirements of species and instead use statistical models that relate current climate to species occurrence data typically parameterized using observations of adult life stages. There have been substantial changes in temperature and climatic water balance during the 20th century in the western United States (Dobrowski et al., 2013). Climate change projections for the 21st century show further increases in temperature and geographic and seasonally varying changes in precipitation (IPCC, 2013). These changes will likely affect the timing and availability of moisture and thus recruitment patterns in western forests.
The distribution of juvenile trees is informative of the climatic tolerances in which a species can maintain a positive population growth rate (Pulliam, 2000; Nitschke & Innes, 2008). Seedlings in particular are vulnerable to drought, herbivory and disease that are tolerated by adults of the same species. For instance, at low elevations in the western United States, desiccation and temperature extremes limit regeneration for even stress-tolerant species (Seidel, 1986; Kolb & Robberecht, 1996). At high elevations, short growing seasons, frost damage, desiccation and photoinhibition result in high seedling mortality rates (Maher & Germino, 2006; Bansal & Germino, 2008). In contrast, adults of many long-lived woody species have broad climatic tolerances and inertia; their distribution may reflect conditions that were suitable for reproduction in the past as opposed to conditions that are suitable now.

Recent studies (Lenoir et al., 2009; Zhu et al., 2011; Bell et al., 2014) have used data on the distribution of juveniles in an attempt to characterize the regeneration niche – the environmental conditions which allow for the establishment of individuals (Grubb, 1977). It is presumed that the regeneration niche occupies a mesic subset of the adult niche (Jackson et al., 2009); however, evidence for this contention is mixed (Eriksson, 2002; Thompson & Ceriani, 2003; Zhu et al., 2011; Bell et al., 2014). For tree species of the western United States, adults may persist at sites (e.g. at their range margins) that may currently be unfavourable for regeneration (Smith et al., 2009). Under these conditions, niche models or mechanistic models calibrated with adult distributions may overestimate the area that can support viable populations and thus may underestimate a species’ exposure to climate change.

An additional challenge for assessing exposure to climate change is accounting for stabilizing processes. If recruitment and mortality rates must balance in order to maintain viable populations, then a stabilizing process is one which promotes this balance (Lloret et al., 2012). Stabilizing mechanisms are aided by traits that reduce the sensitivity of a species to climate shifts (e.g. tolerance, plasticity, phenotypic variability) and through biotic interactions such as facilitation (Lloret et al., 2012). In the context of forest regeneration, tree and shrub cover has been shown to facilitate recruitment by buffering temperature and radiation extremes at sites (e.g. Gómez-Aparicio & Zamora, 2004). However, our understanding of the broad-scale implications of this process is hampered by the fact that biogeographic studies use data describing macroclimate as opposed to microclimate (i.e. climate mediated by vegetation). Studies use gridded climate products derived from weather stations sited in open conditions. Nonetheless, juvenile trees occupy microclimates near the surface where temperature and moisture often deviate from measurements made at standard instrument heights at sites in the open (Von Arx et al., 2013). This discrepancy may result in a systematic bias in how we characterize the climatic dependence of juvenile trees (Harwood et al., 2014) and our expectation of the exposure of species to climate change. For example, recent work suggests that microclimatic buffering can moderate the response of understory plants to macroclimatic warming (De Frenne et al., 2013). This implies that potential climate-driven declines in recruitment of western trees (e.g. Nitschke & Innes, 2008) may be offset to some degree by the moderating effect of forest structure. It also suggests that large-scale losses of forest canopy (e.g. stand-replacing fire) can amplify the effects of climate change.

In addition to exposure, the sensitivity of organisms to climatic shifts should be mediated in part by their traits. Species with traits that promote dispersal (e.g. wind-dispersed seeds) and establishment may help populations keep pace with changing climate (Corlett & Westcott, 2013). In contrast, traits that enhance tolerance to climate shifts or promote the ability of species to take advantage of microclimatic buffering (e.g. shade tolerance) may decouple recruitment from climate drivers. Over time, shifts in the composition of functional traits at the community level will alter ecosystem response to climate change (McGill et al., 2006).

In this study, we relate patterns of tree recruitment in the western United States to climate, forest structure and species traits to assess factors that may influence recruitment under climate change. We begin by asking if juvenile trees (c. 15–100 cm high) show differences in their climatic niche when compared with conspecific adults (> 15 cm in stem diameter) as this may provide evidence of incipient range shifts (Lenoir et al., 2009; Zhu et al., 2011; Bell et al., 2014). We examine how apparent demographic niche differences vary with species traits such as drought and shade tolerance as these are associated with suites of functional traits that may increase or reduce the sensitivity of species to climatic changes (Syphard & Franklin, 2009). Next, we posit that juvenile trees experience microclimate as mediated by forest canopies, as opposed to macroclimate or climate unaffected by vegetation (hereafter ‘climate’). Hence, we indirectly assess the effect of such biotic interactions by including forest structural variables along with climate variables in bioclimatic niche models. We ask if including structural variables in niche models changes the response functions of juvenile trees to climate. This would provide evidence that forest structure may mediate the sensitivity of recruitment to climate.

**METHODS**

**Inventory data**

We used data on tree species occurrences from the USDA Forest Service’s Forest Inventory and Analysis (FIA) programme, a national inventory across land ownerships within the United States. The FIA programme tabulates adult trees, defined as having a diameter at breast height (d.b.h.) > 12.7 cm, and seedlings in each subplot (Woudenberg et al., 2010). Hardwood seedlings are defined as being at least 30.5 cm high with a root collar diameter < 2.5 cm whereas conifer seedlings are defined as being at least 15.2 cm high with a root collar diameter < 2.5 cm. Hereafter we refer to seedlings as juveniles.
The FIA plots used in this analysis came from the 11 western US states and were inventoried between 1984 and 2011 with sampling intensity varying among states and between the analyses we present (demographic niche differences versus recruitment models). We aggregated all subplot data to the plot level. For plots visited more than once, we excluded all but the latest visit. We excluded plots on private land and those showing evidence of tree planting or human disturbance, leaving 33,665 plots. We limited our analyses to species with at least 30 occurrences of both adults and juveniles to ensure adequate statistical representation. Additionally, we excluded species which reproduce principally through asexual means and whose distributions extend far beyond the western United States (e.g. *Populus tremuloides*). This resulted in a total of 62 species.

**Climate data**

Two climate datasets were used in this study, both of which included three bioclimatic variables: minimum temperature ($t_{\text{min}}$), actual evapotranspiration (AET) and climatic water deficit (deficit). Low minimum temperatures and water availability are assumed to constrain high- and low-elevation and latitudinal range margins, respectively, of tree species (Woodward, 1987). AET is a surrogate for productivity (i.e. a measure of the simultaneous availability of moisture and energy), whereas deficit is a measure of drought or unmet atmospheric demand for water (Stephenson, 1990). Estimates of the climatic water balance account for the seasonal timing of availability of water and energy and thus represent a more mechanistic link to the limiting resources that define terrestrial species distributions and productivity (Stephenson, 1990; Gavin & Hu, 2006; Littell et al., 2008).

To assess demographic differences in climatic niches, we used annual summaries of monthly normals for $t_{\text{min}}$, AET and deficit from the period 1976–2005 at 30 arcsec (c. 800 m) resolution as described in Dobrowski et al. (2013) and In Appendix S1 in Supporting Information. Exact coordinates of FIA plots are not publicly available, thus bioclimatic variables at FIA plot locations for the period 1976–2005 were extracted by the US Forest Service Spatial Data Services and provided to us.

The second climate dataset used in modelling current and future recruitment was derived from downscaled climate projections from 14 climate models participating in the Fifth Coupled Model Intercomparison Project (CMIP5). We considered both historical experiments (1950–2005) and experiments run using Representative Concentration Pathway 8.5 (2006–99) to derive climatic water balance metrics at the 2.5 arcmin (c. 4 km) resolution (further details are provided in Appendix S1). For modelling recruitment we required plot coordinates. Therefore we extracted bioclimatic variables using perturbed coordinates that are publicly available in the FIA database. These coordinates have been randomly perturbed by distances not exceeding 1.67 km, but typically within a 0.8-km radius of the actual plot location (McRoberts & Holden, 2005).

**Demographic niche differences**

We characterized climatic niches using means and medians, niche boundaries using the 95th and 5th percentiles and niche tolerance as the difference between the 95th and 5th percentiles of each climate variable from occupied plots for each species and age class. To compare means we used t-tests on climate values from occupied plots between the two age classes. We calculated differences between adult and juvenile medians, 95th and 5th percentiles, and tolerances for each species and then compared these across all species using one-sided paired Wilcoxon signed rank tests. We utilized differences between adult and juvenile climate envelope boundaries as these should be less sensitive to detection errors associated with varying sampling intensity between life stages (Bell et al., 2014). Using linear models, we assessed if demographic niche differences (adult minus juvenile normalized by adult tolerance) at the median and the 5th and 95th percentiles of each climatic distribution, varied by species traits including shade and drought tolerance. Values for shade and drought tolerance were taken from Niinemets & Valladares (2006) and were scaled from one to five, one being least tolerant and five most tolerant. Of the original 62 species, trait data were available for 56.

**Recruitment model overview**

Our recruitment models were designed to describe recruitment patterns within the extant range of each species and are not intended to project range shifts. For a given species, we used generalized linear mixed models (GLMMs) with a logit link function to analyse the presence and absence of juveniles at plot locations where the species (adult or juvenile) was recorded. We used GLMMs rather than generalized linear models (GLMs) because, for many species, variograms of GLM residual error indicated spatial autocorrelation up to a range of 100 km, suggesting the presence of spatially structured processes not explained by our covariates. A gridded (15 arcmin, or 25 km resolution) spatial random intercept was used to account for the variability introduced by such latent processes in the models.

We considered three bioclimatic and three structural covariates. The bioclimatic covariates were previously described and include $t_{\text{min}}$, AET and deficit. The highest correlation between any pair of climate covariates was −0.54 which occurred between deficit and AET. Since locations were visited over a range of years, we used mean values of the climate covariates for the 20 years up to and including the year of each FIA plot visit. We chose 20 years because age data collected at a subset of FIA plots suggest that for all species, 90% of juveniles were 20 years old or less. The structural covariates were: (1) log-transformed live trees per hectare (LITPH), a proxy for density and shading; (2) live tree basal area per hectare ($B_{\text{Aba}}$), a proxy for age and potential competition for resources; and (3) live conspecific basal area per hectare ($B_{\text{Aconspec}}$) a surrogate for the presence of a conspecific seed source and fecundity. All structural variables were calculated...
on a per-plot basis and were fixed to their observed values for projections presented herein (see Appendix S1). Linear and quadratic terms of each of the six covariates were included in model specification. These six covariates were subdivided into three sets of candidate groups: (1) Full – these models could include all six covariates in variable selection; (2) Climate + BAconspecific – these models include the climate covariates and BAconspecific; and (3) Climate – these models only include climate covariates.

Our methods for model selection and prediction uncertainty are an adaptation of those used by Wenger et al. (2013). We considered all possible combinations of covariates within each candidate group (Full, Climate + BAconspecific, Climate); for the Full and Climate + BAconspecific groups, our model selection approach allowed for candidate models that did not include climate covariates. Further detail on model selection methods are presented in Appendix S1.

Current and future projections were made using a Monte Carlo framework to account for multiple sources of uncertainty including: model selection uncertainty; parameter estimation uncertainty; the uncertainty represented by the GLMM random intercept; choice of global climate model (GCM) climate projection; and binomial sampling uncertainty. Model projections were used to produce a vector of probability of juvenile presence at the subset of plot locations at which the species was present. This was then used to make repeated binomial random draws of presence/absence at each location which was averaged to estimate mean juvenile prevalence – the number of plots with juveniles of a given species divided by the total number of plots at which the species was present. Further details on the estimation of uncertainty are presented in Appendix S1.

RESULTS

On average, juveniles of western US tree species have narrower climatic tolerances than their conspecific adults. Of the 62 species we examined, 46 (74%) exhibited a statistically significant difference ($P < 0.05$) in the mean of their distribution between adults and juveniles along at least one climatic axis. Across species, adults usually had higher median values than juveniles for $t_{\text{min}}$ (one-sided paired Wilcoxon signed rank test; $P = 0.0001$) and deficit ($P = 0.003$), whereas no pattern was found for AET ($P = 0.22$). Adults had higher values than juveniles for the 95th percentile of $t_{\text{min}}$ ($P = 0.0001$), deficit ($P < 0.0001$) and AET across all species ($P = 0.02$). For the 5th percentile, adults had higher values for $t_{\text{min}}$ ($P = 0.02$), no difference for deficit ($P = 0.81$) and lower values than juveniles for AET ($P = 0.02$). Lastly, adults had similar tolerances as juveniles for $t_{\text{min}}$ ($P = 0.21$) and larger tolerances for deficit ($P < 0.0001$) and AET ($P = 0.001$).

Demographic niche differences varied by species traits. At average (median) sites, adults had higher deficit values than juveniles for the most shade-intolerant species (Fig. 1). At the driest sites (95th percentile), adults occupied sites with higher deficit values than juveniles across all levels of shade tolerance (Fig. 1) whereas no differences occurred at the wettest sites (5th percentile). For AET, demographic niche differences varied by shade tolerance. The largest differences occurred for shade-tolerant species at the most productive sites (95th percentile) where adults occupied more productive settings than juveniles. In contrast, at the median and least productive sites (5th percentile) juveniles tended to occupy more productive settings for shade-intolerant species (Fig. 1). Lastly, for $t_{\text{min}}$, niche differences varied with shade tolerance; adults were found in warmer settings than juveniles except at the coolest sites (5th percentile) (Fig 1). Demographic niche differences are summarized in Table S1 in Appendix S2.

Climate model projections show widespread increases in $t_{\text{min}}$ and complex changes for the climatic water balance for the coming century (Fig. 2). While projected increases in mean annual precipitation are seen in a majority of models across the northern two-thirds of the western United States, increased precipitation is seasonally asynchronous from increased demand. Thus, increases in deficit are forecast due to a higher vapour pressure deficit congruent with warming. By contrast, changes in AET are more variable, with increases found across most mountainous regions. These increases arise primarily through increased potential evaportranspiration in energy-limited regions during times of the year when water is available.

Recruitment projections varied between species and by model type. Of 56 species for which we had trait data, 47 remained after dropping species with models that exhibited no skill [area under the curve, (AUC) $< 0.55$] or models that did not converge. The set of projections for *Thuja plicata* (western red cedar) presents patterns typical for many species (Fig. 3). First, the probability of juveniles being present at FIA plots shows large spatial variability. Second, uncertainty in model projections increases through time; 90% uncertainty intervals for 2080 include the current observed prevalence. Third, the inclusion of structural variables in niche models reduces the sensitivity of climate response functions (Fig. 4) and thus dampens changes in recruitment through time. Projections for all modelled species are presented in Appendix S4.

Our projections suggest declines in recruitment that vary by species traits. For the Full model set, juvenile prevalence is projected to decline in 2080 (versus that currently observed) from −0.22 to 0.05 (mean $= -0.037$) (Fig. 5). In contrast, from the Climate model set, declines in juvenile prevalence range from −0.36 to 0.09 (mean $= -0.07$). On average projections from the Full model set showed smaller declines and less variance among species than the Climate + BAconspecific set, which in turn showed lower declines and less variance than the Climate set (Fig. 5). Species that had high or low shade and drought tolerance were projected to have larger declines in recruitment than species with intermediate levels of these traits (Fig. 6).

The skill of recruitment models varied between species and by model type. The inclusion of structural covariates increased model skill (Fig S1 in Appendix S3). For the Full model set, AUC values for the best candidate models (derived from
spatially independent cross-validation) varied from 0.57 to 0.87 (mean = 0.69). For comparison, AUC values calculated using simple random partitioning of the training data were higher (mean = 0.82) (results not shown). Within the Full model set, stand structural variables showed greater importance than climate predictors on average (Fig. S2 in Appendix S3). Uncertainty in model projections (the SD of predicted prevalence) for the year 2080 varied among species from 0.02 to 0.19 (mean = 0.07). Model specification uncertainty (0.04) and parameter uncertainty (0.039) were the primary contributors to this followed by GCM uncertainty (0.02).

**DISCUSSION**

**Observed demographic niche differences**

A geographic comparison of the distribution of adult and juvenile trees in the western United States reveals that, on average, juveniles occupy a climatic subset of their conspecific adults. The largest demographic differences occur at species range margins (95th and 5th percentiles of climatic distributions; Fig. 1) but were also apparent at the median of their distributions. This result is consistent with the study by
Bell et al. (2014) which found that juveniles of six western US tree species have narrower climatic tolerances than their conspecific adults. Here we extend this work to a broader range of species and show that demographic niche differences vary as a function of species traits and climatic context.

The mechanisms driving niche differences vary regionally and across the spectrum of species traits. In water-limited systems juveniles were found in more hygric settings, whereas in energy-limited systems adults occupied more productive settings (Fig. 1). For instance, at the xeric end of species climatic distributions (95th percentile for deficit), juveniles consistently occupied moister settings than adults regardless of their shade and drought tolerance (drought tolerance is negatively correlated with shade tolerance; Pearson correlation = −0.77). In contrast, at the most productive sites (95th percentile for AET), adults of shade-tolerant species occupied sites with higher productivity on average than juveniles. These species occur principally in the Pacific Northwest where recruitment may be limited by competition for resources such as light and space (e.g. with moss cover; Harmon & Franklin, 1989). Similarly, niche differences in \( t_{\text{min}} \) were largest for shade-tolerant species with juveniles occupying cooler climates on average than adults. Our results suggest that: (1) demographic niche differences for deficit are apparent at the xeric climatic
margins of a broad range of species; (2) juveniles of shade-tolerant species are found in cooler temperatures than adults – at the most productive sites, they appear to be limited by competition for resources; and (3) minimum temperature does not appear to constrain recruitment in western forests to the same degree that water limitations do.

Species traits mediate recruitment projections

Projected declines in recruitment for this century were most evident for species at the extremes of the shade and drought tolerance spectrum (Fig. 6). At the xeric end of the spectrum, drought-adapted species showed large declines in prevalence because these species often occur near the climatic margins that can support trees (i.e. lower tree line). Species with strong shade tolerance also showed large projected declines, reflecting what is presumably greater sensitivity to warming and increased drought stress projected for the 21st century (Fig. 2).

Species with intermediate tolerance to both shade and drought showed the lowest projected declines in recruitment (Fig. 6). This implies that tolerance to multiple stressors is an important trait that may confer resilience against climatic changes. Our models suggest seven species will see increases in recruitment ($Arbutus$ menziesii, $Calocedrus$ decurrens, $Pinus$ lambertiana, $Umbellularia$ californica, $Cornus$ nutallie, $Abies$ magnifica, $Pinus$ jeffreyi) most of which are endemic to low- to mid-elevation mixed evergreen forests of the California (CA) floristic province. This is consistent with dynamic vegetation model forecasts for the expansion of the mixed evergreen forest type in CA (Lenihan et al., 2003).

Niinemets & Valladares (2006) identify five of the species we examined as tolerant to both drought and shade ($Arbutus$ menziesii, $Calocedrus$ decurrens, $Lithocarpus$ densiflorus, $Chrysolepis$ chrysophylla, $Quercus$ emoryi), four of which are found in mixed evergreen forests of CA. Tolerance to both shade and drought is rare and the propensity of CA to harbour species that tolerate multiple stresses may be due in part to the climate of the state. Like many of the worlds’ mediterranean-climate zones, CA has very high inter-annual variability in precipitation (Dettinger et al., 2011). Under a variable hydroclimate, there
sensitive to these variables (Fig. S3 in Appendix S3). Our intention was to highlight the importance of microclimate and through competition for resources. Indeed, our results suggest that forest structure partly defines the distribution of safe sites, presumably through facilitative effects on recruitment at FIA plots at which the species is present, obviating dispersal constraints. As for the establishment niche, our results are consistent with this framework. In our study, forest structure and productivity covary with climate (Littell et al., 2008) amongst other factors. Thus, if we solely attribute variance in recruitment to climatic variability, while ignoring other proximal drivers such as forest structure, we may confound direct and indirect impacts of climate change and misattribute the processes that constrain recruitment.

Forest structure mediates recruitment projections

Young et al. (2005) posit that the distribution of juveniles can be characterized by the intersection of the adult niche (where a seed source is), the dispersal niche (where seeds can disperse to) and the establishment niche (safe sites for germination and establishment). Our results are consistent with this framework. In our models, the importance of a seed source was clear; basal area of conspecific adults showed the highest average variable importance (Fig. 2 in Appendix S3). In terms of dispersal, we model recruitment at FIA plots at which the species is present, obviating dispersal constraints. As for the establishment niche, our results suggest that forest structure partly defines the distribution of safe sites, presumably through facilitative effects on microclimate and through competition for resources. Indeed, stand basal area and stem density had higher average variable importance than climate variables in our simulations (Fig. 2 in Appendix S3) and a comparison of model projections with observed versus modified structure suggests that regeneration is sensitive to these variables (Fig. 3 in Appendix S3). Our intention in including these predictors is not to directly compare structural variables against climate data in an absolute sense, but instead to speak to what may be an overemphasis on the direct role of climate in mediating range shifts in trees. Our results indicate that models calibrated solely with climate data project declines in recruitment that are 47% larger on average than models that also account for forest structure. These results are consistent with a growing body of work that finds that bioclimatic niche models overestimate range shifts due to missing covariates and/or spatial aggregation in species distributions due to biotic processes (Swanson et al., 2013; Crase et al., 2014). Recruitment patterns of western US trees exhibit spatial aggregation that is probably due to dispersal constraints and biotic interactions such as facilitation. At coarse scales, forest structure and productivity covary with climate (Littell et al., 2008) amongst other factors. Thus, if we solely attribute variance in recruitment to climatic variability, while ignoring other proximal drivers such as forest structure, we may confound direct and indirect impacts of climate change and misattribute the processes that constrain recruitment.

Stabilizing processes and species traits

The moderating influence of forest canopies on climate is well described at the site level in micrometeorological studies (Chen et al., 1993; von Arx et al., 2013) but is not well characterized at broad scales. Tree canopies intercept shortwave radiation, reduce wind speeds and lower the ratio of sensible to latent heat flux (the Bowen ratio). Similarly, moisture in canopies and in the soil reduces the magnitude of diurnal fluctuations in air and soil temperature (Ashcroft & Gollan, 2013; von Arx et al., 2013) – fluctuations that result in seedling mortality. However, few studies quantify these processes over large areas (although see Fridley, 2009; Ashcroft & Gollan, 2013) thus limiting our ability to understand the importance of this stabilizing process at biogeographic scales.

Specific traits allow organisms to take advantage of stabilizing processes, and the traits that can confer resilience to climate change will largely depend on whether sites are disturbed or retain intact forest canopies. For instance, broad-scale densification has been observed in forests of the western US over the past century, driven principally by the suppression of fire in low- and mid-elevation forests where historical fire frequencies were high (Nagel & Taylor, 2005; Miller et al., 2009). This has resulted in shifts in composition in these forests toward shade-tolerant species (Barbour et al., 2007). Species that can regenerate in the shade are more likely to establish in dense forests; these same species are more likely to be able to take advantage of microclimatic buffering than shade-intolerant species. In the absence of disturbance, this feedback mechanism may promote lagged responses to climate change and disequilibrium dynamics (Svenning & Sandel, 2013). Concomitantly, increases in fire extent and severity, increasing temperature and, in many regions, increasing drought favour species that are tolerant of shortened growing seasons and water stress. Climate warming is expected to increase the extent of area burned and the severity of fires (Dillon et al., 2011; IPCC, 2013) and reduce the probability...
of regeneration by removing overstorey vegetation that can moderate near-surface climate. Thus, future fire regimes may promote rapid shifts in vegetation communities by favouring species that can regenerate in exposed sites, survive in canopy or soil seed banks, or readily disperse into areas of high burn severity. Near the climatic margins that can support trees, increasing drought and linked disturbances may lead to the failure of regeneration and ecosystem transitions (Dale et al., 2001; Allen et al., 2010). On balance, the rare set of species that have tolerance to multiple stressors (e.g. shade and drought) should have lower sensitivity to the projected climate changes and perturbations of the future.

**Conservation and management implications**

Our findings highlight the potential for forest management at local to regional scales to mediate regeneration responses to climate change. For example, forest thinning is being used to reduce the likelihood of catastrophic fire losses in western US forests (Safford et al., 2012). Structural manipulations that mitigate the risk of stand-replacing disturbances also maintain viable seed sources and canopy microclimatic buffering (Stevens et al., 2014). However, in areas that are climatically marginal for reproduction, thinning to confer resilience in mature trees should be balanced against potential reductions in recruitment driven by loss of canopy cover and loss of microclimatic buffering.

Our results also inform potential conservation actions such as assisted migration. Our finding that juveniles exhibit a more restricted climatic niche than adults suggest that niche models based on adult distributions will likely overestimate the viability of extant populations and areas suitable for moving species ahead of climate change. Further, conservation actions must consider not only where suitable habitat for a species will be in the future but if the ecosystem can provide the stabilizing processes necessary to support ongoing recruitment.

**Caveats**

Our methods improve on recognized weaknesses common in bioclimatic niche modelling. We use mechanistic predictors (water balance) and probabilistic uncertainty accounting and explicitly consider demographic differences in the species niche. However, limitations of our approach are evident. First, we model regeneration at FIA plots within the extant distribution of each species, and consequently, we do not consider potential range expansions which may offset recruitment declines. Our understanding of dispersal and establishment is rife with uncertainty (Corlett & Westcott, 2013) and our results suggest that stabilizing processes are important and rarely considered. Second, we do not explicitly simulate how climatic changes may influence forest structure into the future. Changes in forest structure may occur due to climate-driven tree mortality (Allen et al., 2010), disturbance, forest management practices and their interaction with climate (Oliver & Morecroft, 2014). Third, we indirectly characterize microclimate using statistical models as opposed to measuring it directly. The latter approach, i.e. direct measurement, is preferable but would require below-canopy weather data which are rare over large areas. Lastly, our approach does not consider the entire reproduction niche (Bykova et al., 2012). Nonetheless, our results emphasize the importance of the establishment phase for understanding climatic constraints on tree distributions and the direct and indirect role of forest structure and species traits in mediating this response.

**CONCLUSIONS**

Climate correlates with species ranges at coarse scales but it exerts influence at the scale of individual plants. This influence is mediated in part by topography, vegetation structure and microclimate (Ashcroft et al., 2009; Dobrowski, 2011). Here we find evidence that forest canopies moderate the sensitivity of recruitment to climatic variation and we posit that the importance of this stabilizing process depends largely on species traits, including their ability to utilize sites with microclimatic buffering. We emphasize that the composition and distribution of forests of the future will depend a great deal on the ability of trees to regenerate at existing sites and colonize and establish at new sites. Existing vegetation composition and structure can both promote or hinder recruitment; this is particularly important for understorey plants such as tree seedlings. Biotic systems are vulnerable to global change but they also have inertia. Understanding the stabilizing processes that promote resilience against climate change and the traits of species that can take advantage of these processes is an important consideration for conservation and management of western US forests.

**ACKNOWLEDGEMENTS**

Support for this research was provided by the National Science Foundation (DEB; 1145985), the Montana Institute on Ecosystems (as supported by NSF EPSCoR grant EPS-1101342), the USDA Forest Service Rocky Mountain Research Station (JV11221635-201), and the USFS Region 5. We are grateful to R. McCullough with the USFS Spatial Data Services for extracting climate data and providing FIA plot data.

**REFERENCES**


Miller, J., Safford, H., Crimmins, M. & Thode, A. (2009) Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. Ecosystems, 12, 16–32.


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

Appendix S1 Supplementary methods.
Appendix S2 Supplementary tables.
Appendix S3 Supplementary figures.
Appendix S4 Species forecasts.

BIOSKETCH

Solomon Dobrowski is an associate professor of landscape ecology. His research interests include the response of forests to climate change, spatio-temporal variability in climate and historical ecology.

Editor: Niklaus Zimmermann