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LETTER

The role of demographic compensation in stabilising marginal tree populations in North America

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Abstract

Demographic compensation—the opposing responses of vital rates along environmental gradients—potentially delays anticipated species' range contraction under climate change, but no consensus exists on its actual contribution. We calculated population growth rate (λ) and demographic compensation across the distributional ranges of 81 North American tree species and examined their responses to simulated warming and tree competition. We found that 43% of species showed stable population size at both northern and southern edges. Demographic compensation was detected in 25 species, yet 15 of them still showed a potential retraction from southern edges, indicating that compensation alone cannot maintain range stability. Simulated climatic warming caused larger decreases in λ for most species and weakened the effectiveness of demographic compensation in stabilising ranges. These findings suggest that climate stress may surpass the limited capacity of demographic compensation and pose a threat to the viability of North American tree populations.

KEYWORDS
demoraphic compensation, integral projection model, plant demography, population growth rate, range limit, vital rate

INTRODUCTION

Every species has a finite geographical range, beyond which the combined contributions of vital rates (i.e. survival, growth, reproduction and recruitment) to its population growth rates (λ) are insufficient to maintain stable populations (Angert, 2006; Ellner et al., 2016). With ongoing climate change, a multitude of species are tracking their shifting suitable habitats, which often yields species range expansions at high latitudinal or elevational edges and range contractions at low latitudinal or elevational edges (Chen et al., 2011; Iverson et al., 2008; Morueta-Holme et al., 2015). However, many species still persist in their original habitats and show no sign of net range shift (Moritz et al., 2008; Tingley et al., 2009). A fundamental question in macroecology and biogeography is how marginal populations manage to persist under deteriorating conditions. Few studies have focused on the possible mechanisms of demographic compensation (Doak & Morris, 2010), which occurs when vital rates respond in opposite directions to each other along an environmental gradient. Perfect 'compensation' of some vital rates can yield stable population size at marginal populations. Even if imperfect, compensation may reduce overall variation in λ across the species' range (Daco et al., 2021; Oldfather & Ackerly, 2019) or over time (Andrello et al., 2020; Compagnoni et al., 2016), potentially allowing populations to persist at low latitudinal or elevational edges of a species' range. Nevertheless, several recent studies have challenged the view that demographic compensation rescues marginal populations (Sheth & Angert, 2018) due to negligible (Dibner et al., 2019; Reed et al., 2021) or even negative (Oldfather et al., 2021) effects on λ. Whether or not and to what extent demographic compensation stabilises marginal populations across spatially and temporally varying environments still remains unclear.

One main explanation for the varying degrees of demographic compensation is that population-level responses to environmental gradients are mediated via correlations between the 'contributions' of each vital rate to among-population variation in λ (Rees & Ellner, 2009), rather than by correlations between the vital rates directly. A high 'contribution' requires high sensitivity of λ to that vital rate and/or high variation in the vital rate among populations (Caswell, 2001; Villellas et al., 2015). As a result, even if vital rates shift in opposite directions along an environmental gradient, the positive contribution of increasing vital rates may be insufficient to offset the negative contribution of other decreasing rates. For example, Sheth and Angert (2018) demonstrated that the impact of increased reproduction of a scarlet monkeyflower along a latitudinal gradient was outweighed by the reduced rates of survival, growth and recruitment, resulting in declining λ towards the southern edge. Moreover, while demographic compensation may result in short-term population stability across a range of moderate environmental conditions, the compensatory increase of one or more vital rates are unlikely to continue indefinitely (Doak & Morris, 2010). If this is the case, population growth will decline beyond a critical environmental threshold, leading to range contractions. Therefore, the complex effects and potential thresholds of demographic compensation require further studies on how demographic processes vary in response to environmental factors across a species range.

Climate and biotic interactions usually affect plant demographic rates differently (Dalgleish et al., 2011; Morris et al., 2020; Rozendaal et al., 2020) and further influence the strength of demographic compensation effect. Climatic warming generally boosts tree growth or reproduction (Benito-Garzón et al., 2013) until warming-induced drought becomes a limiting factor (Babst et al., 2019), which may compensate a concomitant decline in survival (Doak & Morris, 2010). Nevertheless, the strength of these responses varies across species (Oldfather & Ackerly 2019; Sheth & Angert, 2018; Zhang et al., 2015). In addition, biotic interactions at local scales may alter large-scale demographic compensation resulting from climatic conditions, for instance through effects of competition on survival and fecundity (Alexander et al., 2015; Morin et al., 2011). Despite the large body of studies on biotic and abiotic drivers of plant demography, there exists little insights into the compensatory responses to these drivers across species' geographic ranges. Such insights are crucial for gauging species' potential persistence under future climatic conditions.

North American forests provide tremendous ecological, economic and societal benefits (Pan et al., 2011), yet they are becoming increasingly vulnerable to climate change, which may outpace the capacity of many temperate and boreal tree species to keep up via migration (Corlett & Westcott, 2013; Stanke et al., 2021). Recent studies on species occurrences or abundances have revealed that many North American tree species are shifting north (Boisvert-Marsh & de Blois, 2021; Shirk et al., 2018; Woodall et al., 2009), south (Zhu et al., 2012) or west (Fei et al., 2017). Still, many others seem not to shift their ranges at southern edges (Prasad et al., 2020), and the reasons for this remain unclear. One possible reason is that demographic compensation may create pathways to short-term population stability at range edges. Nonetheless, the effort to explore the role of demographic compensation in stabilising tree species distributions is limited. Moreover, whether or not vital rates will be maintained in the same way as the climate continues to warm has been called into question (Briscoe et al., 2019; Morin & Thuiller, 2009). In particular, climate (Davis et al., 2019; Shriver et al., 2021; Stanke et al., 2021; van Mantgem et al., 2009) and neighbourhood competition (Le Squin et al., 2021; Zhang et al., 2015) have increasingly impacted tree demographic rates in North American forests over the recent decades. In addition to the unknown role of demographic compensation in tree

species range limit stabilisation, an unresolved topic in North American forests is how demographic compensation responds to changing climate and competition.

To address these issues, we conducted a continental-scale analysis of demographic performance for 81 North American tree species using 322,338 individual observations from 13,615 long-term forest inventory plots. We first used integral projection models (IPMs; Easterling et al., 2000) to investigate spatial patterns of population growth rate (λ) and evaluated tree species range dynamics based on λ of marginal populations. Second, we used generalised additive models to assess demographic compensation over the range of each tree species and used a randomisation approach to test whether demographic compensation reduces spatial variations in λ. Third, we used perturbation analyses to test which environmental factors are most influential to λ and examined the response of demographic compensation to simulated changes in these factors, as some have been predicted to be particularly important (e.g., temperature at northern limits and competition at southern limits; Louthan et al., 2015). Specifically, we addressed the following three questions: (1) How prevalent is demographic compensation across the geographic ranges of these 81 tree species? (2) To what extent does demographic compensation reduce spatial variations in λ? (3) How do changing climate and plant competition affect demographic compensation? This study is expected to contribute to an increased knowledge of species range stability from a demographic standpoint, providing an important perspective for understanding and anticipating tree diversity and range dynamics in response to ongoing environmental changes.

MATERIALS AND METHODS

Demographic, climate and competition data

Our study covered the continental United States and six Canadian provinces (Figure 1) based on long-term forest inventory data from the USDA Forest Inventory and Analysis (FIA) and Canadian Permanent Sample Plots (PSP) (Supplementary Information, *Country-specific protocols*). For comparisons of demographic performance across species ranges, we applied a set of selection criteria for sampling plots, species and individuals (Supplementary Information, *Data screening criteria*). In brief, we selected the plots from only naturally regenerated stands with no evidence of disturbance and restricted analyses to those species for which sampled plots covered more than half of the latitudinal breadth of Little's distribution maps (Little & Viereck, 1971). We included trees larger than 12.7 cm in DBH (diameter at breast height) as adults and defined recruits as individuals with DBHs >12.7 cm in the current census but <12.7 cm in the previous one. We used a total of 322,338 individuals from 81 tree species and in 13,615 forest plots (Figure S1, Table S1). The number of plots per species ranged from 8 to 3085. The average number of individuals per plot per species was 14, and the average number of censuses per species was 2.3.

We selected three climate variables, including mean warmest month temperature (MWMT), mean coldest month temperature (MCMT) and mean annual precipitation (MAP), all of which we obtained using the ClimateNA v6.21 program (http://climatena.ca, 4-km resolution, Wang et al., 2016). We averaged climate variables for each plot over all years within each census period, using climate data between 1974 and 2018. Within the geographical ranges of most of the 81 tree species, temperature and precipitation generally declined with increasing latitudes (Figure S2). We defined local competition for each individual as the total basal area (BA, m^2/ha) of living surrounding tree individuals within the same plot. Stand-level competition was calculated as the total basal area of living trees per plot. This is a proxy for the combined effect of inter- and intra-specific competition for light and other resources, which is considered as one of the best competition indices (van Mantgem et al., 2009; Zhang et al., 2015).

Population growth rate (λ)

For each species at each plot, we used IPMs (Easterling et al., 2000) to calculate the population growth rate (λ), where vital rates (survival, growth and fecundity) are modelled as continuous functions of individual plant size (DBH). We used a logistic regression model with a binomial error distribution to model survival probability, a Gaussian linear regression to model growth and a zero-inflated Poisson model to model the number of recruits. For each vital rate, we pooled the data from all populations of each species to construct global generalised linear mixed model with fixed effects of tree sizes and climate and competition variables and the random effect of study plot. To decide which environmental variables should enter vital rate models, we carried out an all-subsets regression approach, which fits a series of candidate models that incorporates all combination of environmental variables to identify the 'best' model using the corrected Akaike Information Criterion (AICc) (Supplementary Information). We included quadratic and interaction terms for environmental variables to allow for unimodal vital rate responses. We conducted robustness analyses to verify the effect of vital rate model structure on the output of demographic models and found that the model structure had little influence on the estimates of λ and demographic compensation (Figure S3 & S4). Since no data on each individual's reproductive state are available, we fixed the reproduction probability to 1 for all size classes because the tree sizes in our study were generally larger than the biological thresholds for most

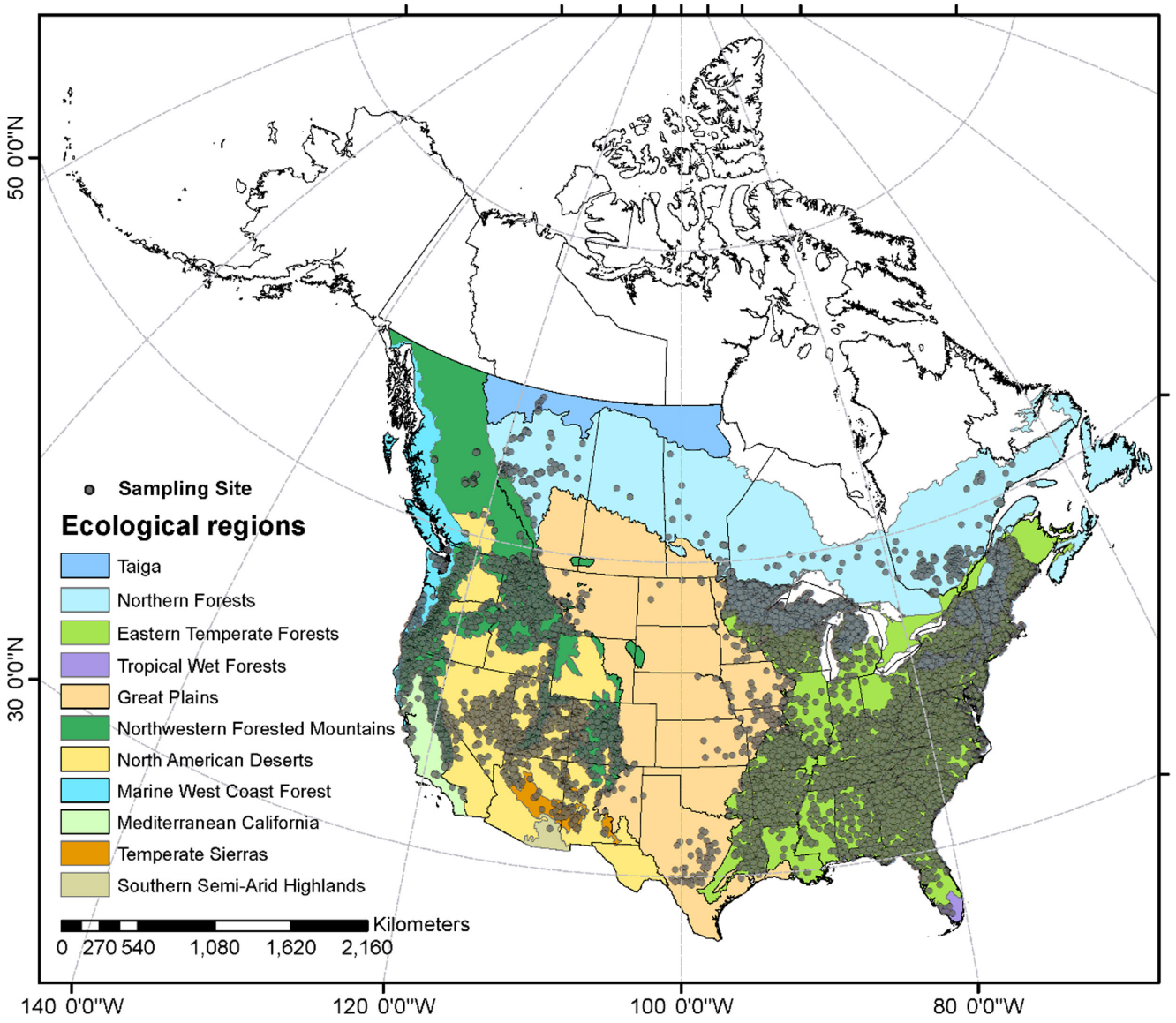

FIGURE 1 Locations of the permanent sampling plots in North America for the 81 tree species

species' reproduction (Clark et al., 2021; Qiu et al., 2021). The size distribution of recruits was described with normal distribution using the empirical mean and standard deviation of the size distribution of recruits in each population. Table S2 shows the final models for each vital rate of all 81 studied species.

We used the fitted vital rate models to build IPMs and calculate λ of each population (Ellner and Rees, 2006). The spatial patterns of λ across species ranges are shown in Figure S5. Since the census interval of plots differs between species (Table S1), we calculated the square root of the λ for species with a 10-year census interval to maintain species comparability with that with 5-year intervals. For plots that were censused more than twice, we calculated the geometric mean of λ over all census intervals. We carried out all analyses in R v4.1.3 (R Core Team, 2022), using R scripts adapted from Sheth and Angert (2018) and Schultz (2022).

Test for demographic compensation

To quantify the prevalence of demographic compensation across the geographic ranges of North American tree species (Q1), we investigated the negative correlations between the contributions of four vital rates (survival probability, growth, the number of recruits and the size distribution of recruits) to among-population differences in λ. We fitted generalised additive models (GAMs) with ln(λ) as the response variable and smoothed functions of vital rate parameters as explanatory variables, as in Sheth and Angert (2018). The proportion of variance in λ was attributed to change in each vital rate parameter (Figure S6), and the contribution of each vital rate was calculated by summing up all its coefficients (e.g. the survival contribution equals the survival slope contribution plus its intercept contribution). The sum of vital rates contributing to variability in ln(λ) were normalised

to 100%. These contributions considered the spatial variation in each vital rate as well as the sensitivity of λ to each vital rate (Zuidema & Franco, 2001).

We used a randomisation approach to determine if the observed data harboured more negative correlations than would be predicted by chance (Villellas et al., 2015). We first assessed the correlations between vital rate contributions using the Spearman rank correlations using one-tailed test. Second, we estimated the relationships after randomly reassigning all vital rate contributions among populations (repeated 10,000 times). Third, we compared the observed numbers of negative correlations to the percentiles of the null distributions obtained via randomisation and calculated the significance level based on the proportion of values in the null distribution that was greater than or equal to the observed number of negative correlations (demographic compensation if the significance level <0.05). In addition, we examined whether species with significant demographic compensation differed in their functional and physiological traits compared to species with no signal of demographic compensation (Supplementary Information).

The effectiveness of demographic compensation

To determine to what extent demographic compensation reduces spatial variations in λ (Q2), we performed a randomisation procedure similar to the approach used in Villellas et al. (2015). First, we randomly reassigned the vital rates if the sum of the contributions of all of the vital rates with which that rate was negatively correlated was greater than the equivalent sum of contributions for its positively correlated rates. We kept the correlations between the pairs of vital rates that both failed to meet the 'sum of contributions' criterion unchanged. We then computed the λ for each population and the among-population variance for the randomised set of vital rate contributions with no significant negative correlations. We repeated this randomisation procedure 10,000 times. In this way, we eliminated negative correlations between contributions of vital rates and obtained a null distribution of λ variance. We inferred the effectiveness of demographic compensation using the ratio of observed λ variance to the median variance of the null distribution (Villellas et al., 2015). A lower ratio means a stronger role of demographic compensation in reducing spatial variation in λ. We then calculated the significance level for the role of demographic compensation as the proportion of values in the null distribution greater than or less than the observed λ variance.

To further reveal the effect of demographic compensation on species ranges, we also identified the trend of species range shifts over the study period. We used non-parametric one-sample Wilcoxon rank test to determine whether the mean λ estimation for northern and southern marginal populations differed statistically from one. We identified marginal populations at each edge as the latitudinal highest or lowest 10% of each species' total number of populations, with a minimum of three marginal populations. If the mean λ of marginal populations was not significantly different from one, we considered the range edge to be in stable; otherwise, we inferred a potential trend of expansion (mean $\lambda > 1$) or contraction (mean $\lambda < 1$). Finally, we estimated the λ variance of each species and used Spearman rank correlations to test if λ differed over latitude among all populations for each species (Table S1).

The effects of climate and competition on demographic compensation

To answer how climate and competition affect tree demographic compensation (Q3), we first identified the predominant environmental factor limiting range edges of each species. We carried out a perturbation analyses (Caswell, 2001) to examine the effect of environmental variables on λ, in which we varied each factor separately while holding all other factors constant at their observed value. We calculated the proportional change in λ by adding 1% of the factor's value to the observed value of the factor (Figure S7). We averaged the elasticity of each factor separately for populations at range edges for each species. The environmental factor with the highest mean relative elasticity value should have the most potential to influence species range shift (Schultz et al., 2022). We identified the predominant climate or competition factors for each species and summed the number of these factors with positive and negative elasticity across 81 tree species. Meanwhile, we conducted an additional perturbation analysis in which we varied each factor separately and determined the absolute change in λ. We chose different perturbation ranges for different factors based on observed and projected environmental change in North America (Wang et al., 2011). We used a reduction and increase of 2°C with an interval of 0.5°C for MWMT and MCMT; 200 mm with an interval of 50 mm for MAP; 20% with an interval of 5% for BA. We calculated the changes in the mean λ of marginal populations, λ variance across the species range and the effectiveness of demographic compensation (the ratio of observed λ variance to median of the null distribution) for each level of perturbation.

RESULTS

The prevalence of demographic compensation across tree species ranges

Only 25 of 81 species had indications of significant demographic compensation (Table 1). When negative correlations between contributions of vital rates were

TABLE 1 Demographic compensation and its effectiveness on reducing the variance in λ across tree species ranges. Only results for species exhibiting demographic compensation are shown here

Species	Demographic compensation[a]						Significance[b]	Effectiveness[c]
	Survival vs. growth	Survival vs. number of recruits	Survival vs. size distribution of recruits	Growth vs. number of recruits	Growth vs. size distribution of recruits	Number of recruits vs. size distribution of recruits		
Abies balsamea	0.339	0.023	**−0.082*****	0.101	**−0.142*****	**−0.189*****	**0.000**	**0.470*****
Abies magnifica	−0.007	−0.148	**−0.371***	**−0.331***	**−0.324***	0.787	**0.000**	0.952
Acer rubrum	0.176	0.079	−0.004	0.168	**−0.061*****	**−0.400*****	**0.021**	1.141
Betula alleghaniensis	0.204	−0.010	−0.077	0.174	**−0.279*****	**−0.786*****	**0.034**	1.306
Betula papyrifera	0.499	0.072	**−0.114***	0.200	**−0.204*****	**−0.809*****	**0.000**	**0.339*****
Carya alba	−0.014	0.115	−0.051	0.152	**−0.183****	**−0.852*****	**0.048**	1.020
Fagus grandifolia	**−0.193*****	−0.012	0.044	−0.060	−0.030	**−0.190*****	**0.034**	**0.231*****
Juniperus virginiana	0.185	0.038	−0.051	0.196	**−0.184*****	**−0.548*****	**0.034**	**0.415*****
Nyssa aquatica	0.269	0.171	**−0.183***	0.190	**−0.186***	**−0.940*****	**0.000**	**0.461***
Pinus albicaulis	**−0.380****	0.040	**−0.273***	**−0.448*****	−0.144	0.040	**0.002**	**0.440*****
Pinus banksiana	0.391	0. 113	−0.090	0.272	**−0.228*****	**−0.846*****	**0.028**	3.448
Pinus contorta	**−0.410*****	0.018	0.038	**−0.071***	**−0.108****	0.894	**0.000**	**0.322*****
Pinus edulis	0.226	0.060	**−0.064****	0.176	**−0.193*****	**−0.818*****	**0.034**	**0.708*****
Pinus flexilis	0.201	0.111	**−0.312***	0.232	**−0.415****	**−0.463****	**0.002**	6.544
Pinus palustris	−0.169	**−0.249***	0.077	0.244	0.041	**−0.554*****	**0.038**	**0.165*****
Pinus rigida	0.102	0.407	**−0.406*****	0.108	−0.111	**−0.984*****	**0.046**	**0.139*****
Pinus virginiana	0.468	0.198	−0.044	0.320	**−0.106***	**−0.372*****	**0.020**	**0.058*****
Populus grandidentata	0.336	0.183	**−0.170*****	0.281	**−0.294*****	**−0.900*****	**0.006**	2.694
Quercus coccinea	0.372	0.124	−0.147	0.184	**−0.185***	**−0.933*****	**0.048**	**0.278*****
Quercus rubra	**0.111*****	**−0.235*****	**−0.227*****	−0.014	**−0.040**	0.887	**0.044**	**0.160*****
Quercus velutina	**−0.251*****	0.137	−0.056	**−0.094***	0.037	0.350	**0.038**	**0.416*****
Robinia pseudoacacia	**−0.278***	**−0.337***	**−0.348***	0.088	0.086	0.995	**0.002**	1.251
Tsuga canadensis	0.207	0.129	−0.023	0.201	**−0.104*****	**−0.371*****	**0.039**	**0.775*****
Ulmus alata	**−0.372*****	−0.133	0.031	−0.014	0.127	**−0.616*****	**0.036**	**0.787*****
Ulmus americana	0.253	0.043	−0.008	0.094	−0.136*	**−0.832*****	**0.030**	1.928

[a]The asterisks indicate the *p*-values of Spearman correlation test for each pair of vital rates: $^{***}p < 0.001$; $^{**}0.001 < p < 0.01$; $^{*}0.01 < p < 0.05$. Significant negative correlation appears in bold.

[b]To test whether demographic compensation occurred by chance, the significance of demographic compensation was calculated as the proportion of values in null distribution greater than or equal to the observed proportion of significant negative correlations. 'Strong' demographic compensation (i.e. the proportion smaller than 0.05) appears in bold.

[c]The effect of demographic compensation on λ variance is analysed by calculating the ratio by the variance found in λ in nature to the median of the variance in randomisations. The smaller the ratio, the stronger is the effectiveness of demographic compensation on reducing λ variance. The *p*-values are the proportion of values in the null distribution that were smaller than the observed λ variance: $^{***}p < 0.001$; $^{**}0.001 < p < 0.01$; $^{*}0.01 < p < 0.05$. Significant effectiveness appears in bold.

detected, they mostly involved the size distribution of recruits. Using bigtooth aspen (*Populus grandidentata*) as an example of strong compensation (Figure 2; Table 1), we found three significant negative correlations out of six possible pairwise correlations: larger recruit size toward low-latitude range edges contributed positively to variation in λ, but this was offset by negative contributions of survival probability, growth and the number of recruits. The observed proportion of negative correlations for this species was significantly higher than expected by chance ($p = 0.006$), indicating significant demographic compensation between vital rates among populations. Plant functional and physiological traits did not differ significantly between the 25 species with compensation and other species with no signal of compensation (Figure S8).

The effectiveness of demographic compensation at reducing spatial variation in λ

In total, 35 (43%) of the studied 81 tree species showed patterns of population growth consistent with population stability at both northern and southern edges (Figure 3). The degree of among-population λ variation was small, ranging from 0.0001 for *Populus deltoides* to 0.0861 for *Gleditsia triacanthos* (Table S1; Figure S5). No significant correlations were found between λ and latitude for most tree species (Table S1). The GAMs revealed that variation in λ across 81 tree species' ranges were best explained by variation in individual plant survival among populations (61%; Figure S6), followed by variance in the number of recruits (19%) and growth (12%). Variance in the size distribution of recruits (8%) explained the small remaining variation in λ.

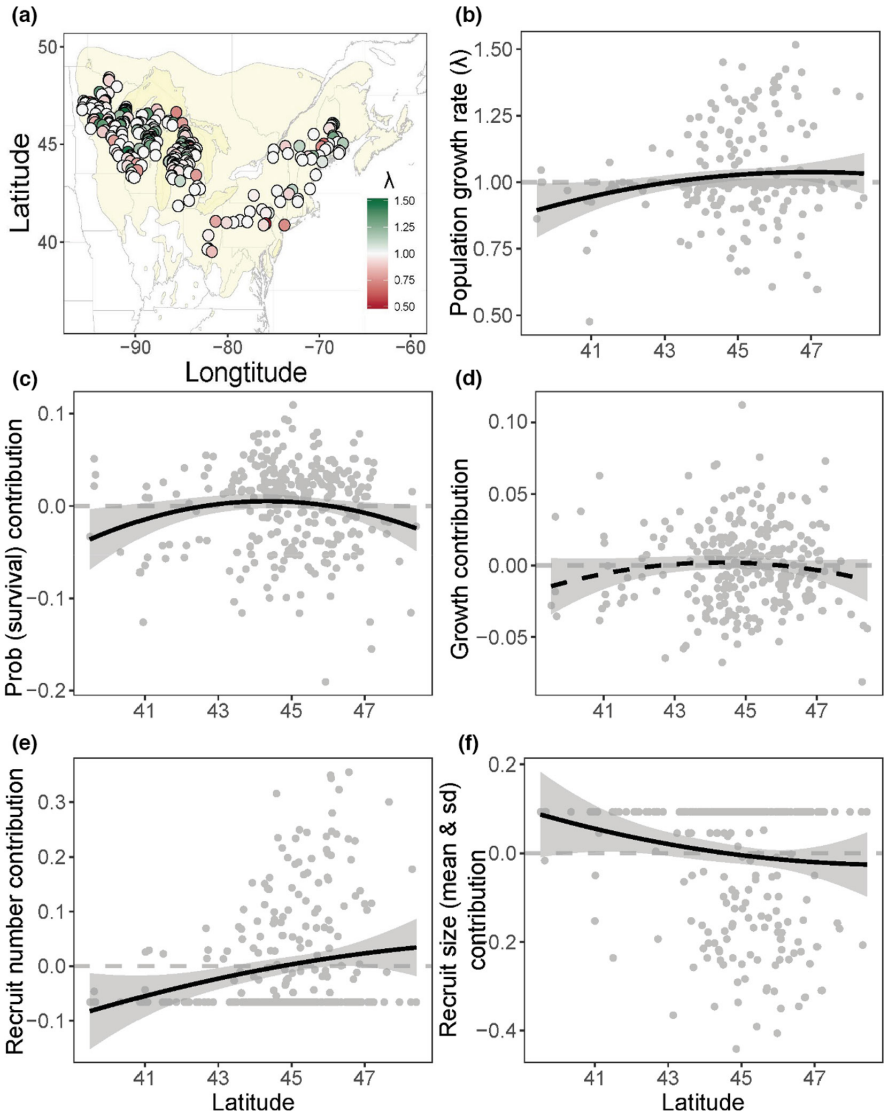

FIGURE 2 (a) The distributions of population growth rate (λ), with green colors indicating high λ and red colors indicating low λ, (b) the latitudinal trend of λ and (c–f) population-specific contributions of vital rates to among-population variance in λ for bigtooth aspen (*Populus grandidentata*) as an example. Solid and dashed lines represent linear and quadratic terms (based on best linear models) with $p < 0.05$ and $p > 0.05$, respectively. The yellow polygon in the distribution map (a) is the species distributional range by Little and Viereck (1971)

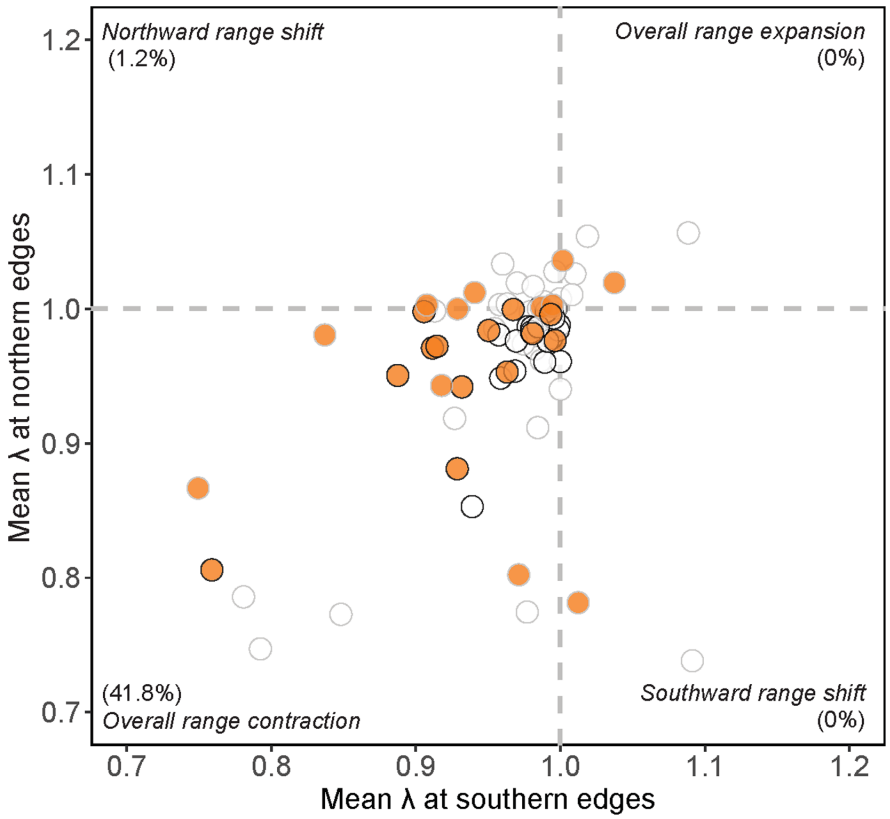

FIGURE 3 Potential trends of range shifts for the 81 tree species, based on the output of integral projection models. The four-quadrant diagram shows the potential range shifts. Percentages in the quadrants summarise the proportion of species strongly falling into the corresponding cases (black border) based on the mean λ estimation for northern or southern marginal populations differing statistically from one (non-parametric one-sample Wilcoxon rank test). The remaining species (grey border) are displayed at the position of their average but are not statistically distinguishable from range stability at their northern edges (49.4%), southern edges (50.6%) or both edges (43.2%). Species exhibiting demographic compensation are indicated in orange and others are in white. Information on the mean λ of marginal populations is shown in Table S1

Demographic compensation greatly reduced among-population variation in λ in 16 of the 25 species exhibiting a sign of demographic compensation (Table 1). The λ variance estimated from the observed data was 38.5% on average (for the 16 species) of the median variance in the random permutations, implying that demographic compensation reduced the λ variance by approximately two-thirds. Despite this, 11 of the 16 species still exhibited a potential tendency of range contraction in the southern edges (mean $\lambda < 1$, $p < 0.05$) (Table S1). The same tendency was observed for 15 of the 25 species exhibiting demographic compensation (Table S1).

The responses of demographic compensation to climate and competition

Simulated proportional increases in MWMT had the greatest negative impact on population growth rates of the 81 species (Figure 4 and S7). These results were consistent when we examined all populations across the range and the subset of marginal populations at either range edge. The changes in λ also had greater associations with MWMT than with the other factors for the species exhibiting demographic compensation (Figure 4).

When simulating an increased MWMT by 2℃, mean λ of marginal populations declined in eight of the sixteen species (Figure 5a, c), with *Pinus albicaulis* showing the strongest response (−0.104 and −0.050 λ/℃ at the northern and southern edges, respectively). Correspondingly, the effectiveness of demographic compensation decreased with warming in these eight species (Figure 5e). In contrast to temperature patterns, increasing local competition resulted in minimal changes in mean λ and the effectiveness of demographic compensation (Figure 5b,d,f). When MCMT was raised, we observed similar patterns of weakened demographic compensation in *P. albicaulis* (Figure S9e), and an increase in MAP had a greater effect on the effectiveness of demographic compensation than in other species (Figure S9f).

DISCUSSION

Limited role of demographic compensation for tree species in North America

Species ranges can encompass enormous variations along environmental gradients, such that vital rates and population growth rates (λ) are apt to change geographically

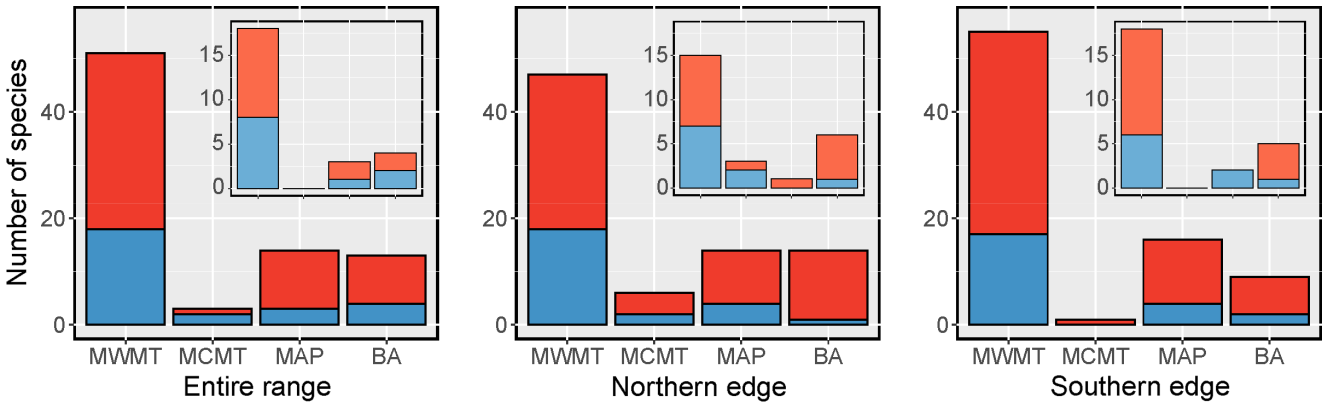

FIGURE 4 Elasticity of λ to predominant environmental drivers for 81 studied tree species (a) across their entire distribution ranges, (b) at northern edges and (c) at southern edges. Inset: The frequency of relative elasticity for the 25 species exhibiting demographic compensation. Shown are species counts of elasticity sign (red: negative; blue: positive) for the environmental factor with the largest mean elasticity for the species (Figure S5). Abbreviations: MWMT (mean warmest month temperature); MCMT (mean coldest month temperature); MAP (mean annual precipitation); BA (total basal area of neighbour trees per unit area)

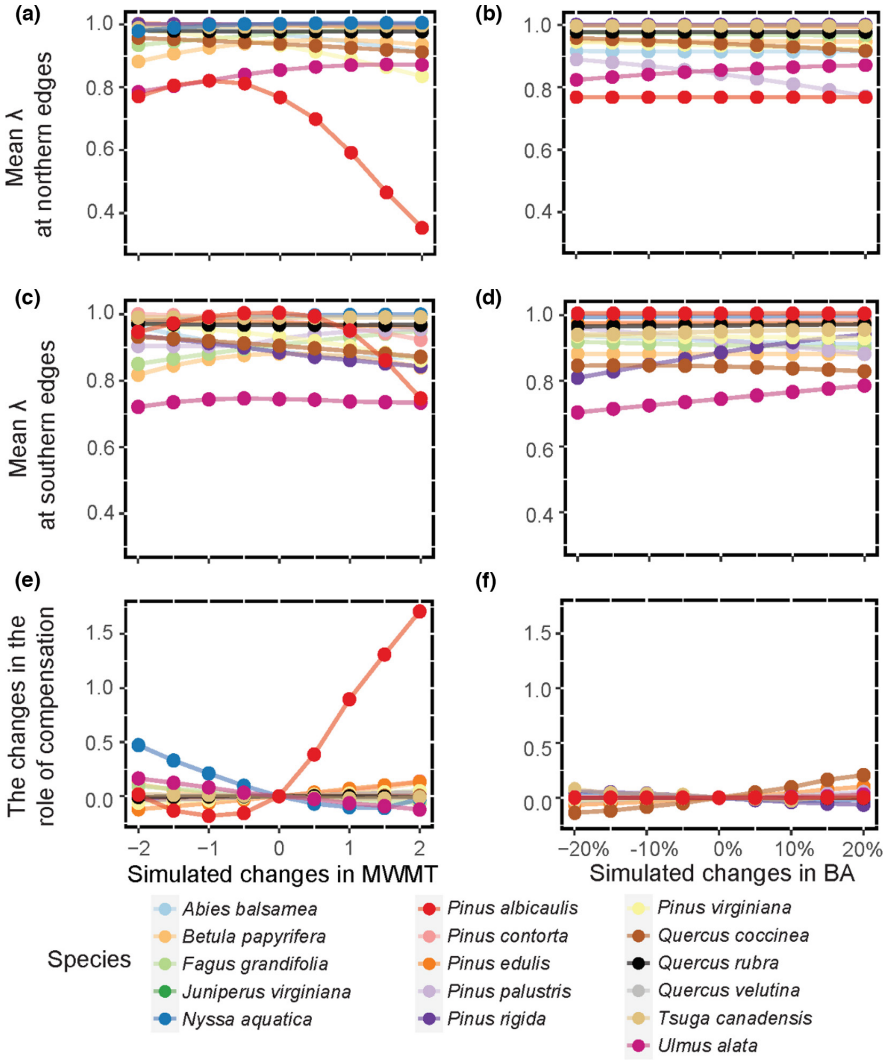

FIGURE 5 (a–d) Mean λ at range edges and (e, f) the changes in the effectiveness of demographic compensation in response to simulated changes in mean warmest month temperature (MWMT) and total basal area (BA) for 16 species exhibiting significant effectiveness of demographic compensation. Each line corresponds to one species, and colors defined in the legend apply to all panels

(Tredennick et al., 2018). Temperature and precipitation dropped significantly with rising latitudes within the geographical ranges of most of the 81 North American tree species we studied, but there was little spatial variation in λ and no significant trends along latitudinal gradients. Another continental-scale study analysis of two North American tundra plants revealed a similar trend of stable performance despite variable environment across the species ranges (Doak & Morris, 2010). A plausible explanation for this is demographic compensation, which involves opposite responses of vital rates to the same environmental gradient (Villellas et al., 2015). Indeed, we found that demographic compensation could effectively reduce spatial variations in λ. However, the compensatory responses were not universal across the 81 studied species' geographic ranges, and there were few commonalities in the species that exhibiting demographic compensation based on their functional and physiological traits. This is surprising, because half of species with demographic compensation are in the Pinaceae family and thus might be adapted to respond quickly to changes in their environment (Turner et al., 2019). This suggests that the observed pattern of similar λ across species ranges for most of these species is more likely to be caused by other buffering mechanisms, such as local adaptation or plasticity (Angert et al., 2020; Laughlin et al., 2020). Consistent with previous studies (Reed et al., 2021; Sheth & Angert, 2018), our findings imply that demographic compensation cannot rescue marginal populations in our study system.

Demographic compensation is a function of both among-population variance of different vital rates as well as the sensitivity of λ to such variance (Villellas et al., 2015). The λ of long-lived organisms, such as trees, is generally sensitive to survival rate (Schultz et al., 2022; Yang et al., 2018). Natural selection tends to minimise variation in those vital rates to which population growth is most sensitive (Hilde et al., 2020; Pfister, 1998; Zuidema & Franco, 2001). Thus, our results revealed that, when compared to other measured vital rates, variations in survival among populations contributed most to the geographical variations in λ, despite the fact that spatial variance in survival rate is minor. However, recruitment rates were most frequently involved in demographic compensation in this study, which was likely due to their high among-population variance. Meanwhile, the low frequency of significant negative relationships between contributions of survival and growth indicated that compensatory change between survival and growth is unlikely to be a general phenomenon in tree species in North America.

Potential range shifts driven largely by warmest temperature

The distributional dynamics of temperate and boreal forests have attracted considerable attention due to their high levels of biodiversity and slow migration rates. Despite different species varying in their responses to climatic and competition factors, there was a clear sign that climate had a greater impact on tree demographic performance than local competition at tree range edges. Increasing warmest temperature was the key potential force of driving changes in λ across ranges among predictor variables, although other unmeasured aspects of microhabitats, such as light environment or edaphic conditions may also be important (Lloret et al., 2012; Zimmermann et al., 2009). This implies that populations throughout the range of a given species, not just those at the warmer edges, may be vulnerable to ongoing and future warming.

The observed rising temperatures in North America (Seager & Vecchi, 2010), declining tree populations in temperate and boreal forests (Stanke et al., 2021; Zhang et al., 2015), and the widely reported extinction debts associated with climate warming (Loarie et al., 2009; Talluto et al., 2017) raise the question of whether these cold-adapted species are approaching or even have crossed a high-temperature tipping point. Plant responses to climate warming are highly tied to their climatic tolerances at a local scale (Bisbing et al., 2020; Zellweger et al., 2020). If local adaptation is strong, the range of environmental tolerances in local populations may be much less than the range of environmental tolerances in the species as a whole (Angert et al., 2011). If this is the case, locally adapted populations may be particularly vulnerable to climate change regardless of their location within the range (Peterson et al., 2018). Thus, even while the 43% of the species tested exhibited a pattern consistent with range stability, the fact that simulated warming tends to have a strong negative influence on λ suggests that the warmest temperatures may soon be out of species suitable thermal ranges (Nomoto & Alexander, 2021).

Weakening effectiveness of demographic compensation with warming

To the best of our knowledge, this is the first attempt to assess the response of range-wide demographic compensation in multiple tree species to continuous climatic change at a continental scale. Our findings suggest that the most prevalent scenario involves a diminishing role of compensation and declining marginal populations. Half of the tree species that exhibit demographic compensation fall into this category: *Abies balsamea*, *Betula papyrifera*, *Pinus albicaulis*, *Pinus contorta*, *Pinus edulis*, *Pinus rigida*, *Pinus virginiana* and *Quercus coccinea*. They may be at high demographic vulnerability as a result of lack of adequate countervailing effects from a compensatory increase in vital rates with climate warming. The efficiency of compensation is reinforced for the second group of species, represented by *Fagus grandifolia*, *Nyssa*

aquatica, *Pinus palustris*, *Quercus rubra*, *Tsuga canadensis* and *Ulmus alata*, and growth rates of marginal populations are increased, indicating that they have the potential to benefit from climatic warming. Moreover, for a few species, such as *Juniperus virginiana* and *Quercus velutina*, there were no changes in their survival, growth and recruitment rates with warming, implying that they have low threats by climatic warming in the near future.

Demographic compensation is unlikely to last continuously as a means of buffering populations against changing environmental conditions (Doak & Morris, 2010). Once a tipping point is crossed, after which demographic rates no longer compensate, this would cause a significant decline in populations and range-wide losses in occupancy or abundance (Peterson et al., 2018). We discovered a potential sign for such a climatic tipping point with *P. albicaulis* (Figure 5), a temperate plant that is fragmented distributed in western North America. This species had the most significant negative reaction to simulated warming, indicating that its populations may have minimal ability to cope with in situ climate change (Anderson & Wadgymar, 2020). Warming considerably weakens the potential of demographic compensation to rescue marginal populations for *P. albicaulis* across the simulated range of mean warm month temperature with an obvious turning point near to the observed value. That is, a tree species with similar demography to *P. albicaulis* may be rapidly approaching a tipping point of high temperature, at which species may lose all demographic buffering effects. Although their long life span allows tree species to persist for a certain period after climatic tipping points being surpassed, this accelerating population decline could culminate in a higher extinction risk to cold-adapted species in temperate and boreal forests (De Frenne et al., 2013; Gottfried et al., 2012).

Caveats and limitations

The current findings have several limitations in their generalisability. First, our estimations are based on large-sized trees and, thus, may have underestimated the prevalence and the strength of demographic compensation since compensation is expected to be stronger for small-sized trees (Benito-Garzón et al., 2013; Canham & Murphy 2016). Incorporating information from long-term seedling monitoring and tree fecundity (Clark et al., 2021) into demographic compensation could provide deep understanding of the dynamics of species ranges in the context of global change. Second, temporal variability in vital rates driven by expected future increasing frequencies of extreme climatic events (Andrello et al., 2020; Lloret et al., 2012), along with short time windows of available tree demographic observations relative to the lifespan of tree species, makes it challenging to estimate long-term stability of species geographic ranges. Recently proposed hierarchical modelling frameworks integrating demographic data and complementary information into the joint probability distribution of data and parameters offer promising ways to address this challenge (Evans et al., 2016). Finally, the balance between generalisation and appropriate specificity should to be carefully considered when describing species-specific demography as flexibly as possible. Our selection of environmental variables used for all species imply that models constructed here for the purpose of a comparative study on demographic compensation will be different from those that might be constructed for other purposes or in studies focusing on single species. Although IPMs are increasingly used in demographic studies, their predictions have only rarely been verified (Doak et al., 2021; Ramula et al., 2009). More model validation efforts from other perspectives, for instance using (independent) presence/absence data of simulated species across environmental ranges (Schultz et al., 2022), may allow evaluating whether and when demographic models capture population performance.

CONCLUSION

Understanding the underlying mechanisms for species distributional ranges and possible range shifts can be improved by examining how trade-offs between vital rates affect populations in response to environmental changes. We investigated the generalities and effectiveness of demographic compensation over the ranges of 81 tree species in North America. Demographic compensation among later life stages is uncommon among North American tree species and if present, is insufficient to rescue marginal tree populations. Population growth rates are primarily negatively sensitive to the MWMT throughout most tree species' ranges, indicating that they may have already exceeded their suitable thermal ranges. Together, declining marginal populations and a weakened role for demographic compensation in response to simulated warming imply that thermal stress may outweigh the buffering effect of compensatory changes, making tree species more demographically vulnerable to future climate change. Our findings thus serve as a cautionary note on the growing demographic vulnerability of temperate and boreal tree species across North America.

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AUTHORSHIP

JZ and XY designed the research with input from ALA. XY analysed the data with advice from JZ, ALA and PAZ. The manuscript was written by XY and JZ with advice from ALA, PAZ, FH, SH, SLL, SZL and NIC.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

No new data were used in this analysis. All the R scripts and the example data used in analyses are deposited in Figshare digital repository (https://doi.org/10.6084/m9.figshare.19687521).

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REFERENCES

Alexander, J.M., Diez, J.M. & Levine, J.M. (2015) Novel competitors shape species' responses to climate change. *Nature*, 525, 515–518.

Anderson, J.T. & Wadgymar, S.M. (2020) Climate change disrupts local adaptation and favours upslope migration. *Ecology Letters*, 23, 181–192.

Andrello, M., Villemereuil, P., Carboni, M., Busson, D., Fortin, M.-J., Gaggiotti, O.E. et al. (2020) Accounting for stochasticity in demographic compensation along the elevational range of an alpine plant. *Ecology Letters*, 23, 870–880.

Angert, A.L. (2006) Demography of central and marginal populations of monkeyflowers (*Mimulus cardinalis* and *M. lewisii*). *Ecology*, 87, 2014–2025.

Angert, A.L., Bontrager, M.G. & Ågren, J. (2020) What do we really know about adaptation at range edges? *Annual Review of Ecology, Evolution, and Systematics*, 51, 341–361.

Angert, A.L., Sheth, S.N. & Paul, J.R. (2011) Incorporating population-level variation in thermal performance into predictions of geographic range shifts. *Integrative and Comparative Biology*, 51, 733–750.

Babst, F., Bouriaud, O., Poulter, B., Trouet, V., Girardin, M.P. & Frank, D.C. (2019) Twentieth century redistribution in climatic drivers of global tree growth. *Science Advances*, 5, eaat4313.

Benito-Garzón, M., Ruiz-Benito, P. & Zavala, M.A. (2013) Interspecific differences in tree growth and mortality responses to environmental drivers determine potential species distributional limits in Iberian forests. *Global Ecology and Biogeography*, 22, 1141–1151.

Bisbing, S.M., Urza, A.K., Buma, B.J., Cooper, D.J., Matocq, M. & Angert, A.L. (2020) Can long-lived species keep pace with climate change? Evidence of local persistence potential in a widespread conifer. *Diversity and Distributions*, 27, 296–312.

Boisvert-Marsh, L. & de Blois, S. (2021) Unravelling potential northward migration pathways for tree species under climate change. *Journal of Biogeography*, 48, 1088–1100.

Briscoe, N.J., Elith, J., Salguero-Gómez, R., Lahoz-Monfort, J.J., Camac, J.S., Giljohann, K.M. et al. (2019) Forecasting species range dynamics with process-explicit models: matching methods to applications. *Ecology Letters*, 22, 1940–1156.

Canham, C.D. & Murphy, L. (2016) The demography of tree species response to climate: seedling recruitment and survival. *Ecosphere*, 7, e01424.

Caswell, H. (2001) *Matrix population models: construiction, analysis, and interpretation*, 2nd edition. Sunderland, MA: Sinauer Associates.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024–1026.

Clark, J.S., Andrus, R., Aubry-Kientz, M., Bergeron, Y., Bogdziewicz, M., Bragg, D.C. et al. (2021) Continent-wide tree fecundity driven by indirect climate effects. *Nature Communications*, 12, 1242.

Compagnoni, A., Bibian, A.J., Ochocki, B.M., Rogers, H.S., Schultz, E.L., Sneck, M.E. et al. (2016) The effect of demographic correlations on the stochastic population dynamics of perennial plants. *Ecological Monographs*, 86, 480–494.

Corlett, R.T. & Westcott, D.A. (2013) Will plant movements keep up with climate change? *Trends in Ecology & Evolution*, 28, 482–488.

Daco, L., Colling, G. & Matthies, D. (2021) Altitude and latitude have different effects on population characteristics of the widespread plant *Anthyllis vulneraria*. *Oecologia*, 197(2), 1–13.

Dalgleish, H.J., Koons, D.N., Hooten, M.B., Moffet, C.A. & Adler, P.B. (2011) Climate influences the demography of three dominant sagebrush steppe plants. *Ecology*, 92, 75–85.

Davis, K.T., Dobrowski, S.Z., Higuera, P.E., Holden, Z.A., Veblen, T.T., Rother, M.T. et al. (2019) Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *Proceedings of the National Academy of Sciences*, 116, 6193–6198.

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, M. et al. (2013) Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences*, 110, 18561–18565.

Dibner, R.R., Peterson, M.L., Louthan, A.M. & Doak, D.F. (2019) Multiple mechanisms confer stability to isolated populations of a rare endemic plant. *Ecological Monographs*, 89, e01360.

Doak, D.F. & Morris, W.F. (2010) Demographic compensation and tipping points in climate-induced range shifts. *Nature*, 467, 959–965.

Doak, D.F., Waddle, E., Langendorf, R.E., Louthan, A.M., Isabelle Chardon, N., Dibner, R.R. et al. (2021) A critical comparison of integral projection and matrix projection models for demographic analysis. *Ecological Monographs*, 91, e01447.

Easterling, M.R., Ellner, S.P. & Dixon, P.M. (2000) Size-specific sensitivity: applying a new structured population model. *Ecology*, 81, 694–708.

Ellner, S.P., Childs, D.Z. & Rees, M. (2016) *Data-driven modelling of structured populations: A practical guide to the integral projection model*. Switzerland: Springer.

Ellner, S.P. & Rees, M. (2006) Integral projection models for species with complex demography. *The American Naturalist*, 167, 410–428.

Evans, M.E., Merow, C., Record, S., McMahon, S.M. & Enquist, B.J. (2016) Towards process-based range modeling of many species. *Trends in Ecology & Evolution*, 31, 860–871.

Fei, S., Desprez, J.M., Potter, K.M., Jo, I., Knott, J.A. & Oswalt, C.M. (2017) Divergence of species responses to climate change. *Science Advances*, 3, e1603055.

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J.L. et al. (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2, 111–115.

Hilde, C.H., Gamelon, M., Sather, B.-E., Gaillard, J.-M., Yoccoz, N.G. & Pelabon, C. (2020) The demographic buffering hypothesis: evidence and challenges. *Trends in Ecology & Evolution*, 35, 523–538.

Iverson, L.R., Prasad, A.M., Matthews, S.N. & Peters, M. (2008) Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management*, 254, 390–406.

Laughlin, D.C., Gremer, J.R., Adler, P.B., Mitchell, R.M. & Moore, M.M. (2020) The net effect of functional traits on fitness. *Trends in Ecology & Evolution*, 35, 1037–1047.

Le Squin, A., Boulangeat, I. & Gravel, D. (2021) Climate-induced variation in the demography of 14 tree species is not sufficient to explain their distribution in eastern North America. *Global Ecology and Biogeography*, 30, 352–369.

Little, E.L. & Viereck, L.A. (1971) *Atlas of United States trees: Conifers and important hardwoods*. Washington, DC: U.S. Department of Agriculture, Forest Service.

Lloret, F., Escudero, A., Iriondo, J.M., Martinez-Vilalta, J. & Valladares, F. (2012) Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology*, 18, 797–805.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, 462, 1052–1055.

Louthan, A.M., Doak, D.F. & Angert, A.L. (2015) Where and when do species interactions set range limits? *Trends in Ecology & Evolution*, 30, 780–792.

Morin, X., Fahse, L., Scherer-Lorenzen, M. & Bugmann, H. (2011) Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters*, 14, 1211–1219.

Morin, X. & Thuiller, W. (2009) Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology*, 90, 1301–1313.

Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C. & Beissinger, S.R. (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, 322, 261–264.

Morris, W.F., Ehrlén, J., Dahlgren, J.P., Loomis, A.K. & Louthan, A.M. (2020) Biotic and anthropogenic forces rival climatic/abiotic factors in determining global plant population growth and fitness. *Proceedings of the National Academy of Sciences*, 117, 1107–1112.

Morueta-Holme, N., Engemann, K., Sandoval-Acuña, P., Jonas, J.D., Segnitz, R.M. & Svenning, J.-C. (2015) Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proceedings of the National Academy of Sciences*, 112, 12741–12745.

Nomoto, H.A. & Alexander, J.M. (2021) Drivers of local extinction risk in alpine plants under warming climate. *Ecology Letters*, 24, 1157–1166.

Oldfather, M.F. & Ackerly, D.D. (2019) Microclimate and demography interact to shape stable population dynamics across the range of an alpine plant. *New Phytologist*, 222, 193–205.

Oldfather, M.F., Koontz, M.J., Doak, D.F. & Ackerly, D.D. (2021) Range dynamics mediated by compensatory life stage responses to experimental climate manipulations. *Ecology Letters*, 24, 772–780.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A. et al. (2011) A large and persistent carbon sink in the world's forests. *Science*, 333, 988–993.

Peterson, M.L., Doak, D.F. & Morris, W.F. (2018) Both life-history plasticity and local adaptation will shape range-wide responses to climate warming in the tundra plant Silene acaulis. *Global Change Biology*, 24, 1614–1625.

Pfister, C.A. (1998) Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences*, 95, 213–218.

Prasad, A., Pedlar, J., Peters, M., McKenney, D., Iverson, L., Matthews, S. et al. (2020) Combining US and Canadian forest inventories to assess habitat suitability and migration potential of 25 tree species under climate change. *Diversity and Distributions*, 26, 1142–1159.

Qiu, T., Aravena, M.-C., Andrus, R., Ascoli, D., Bergeron, Y., Berretti, R. et al. (2021) Is there tree senescence? The fecundity evidence. *Proceedings of the National Academy of Sciences*, 118, e2106130118.

R Core Team (2022) *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Ramula, S., Rees, M. & Buckley, Y.M. (2009) Integral projection models perform better for small demographic data sets than matrix population models: a case study of two perennial herbs. *Journal of Applied Ecology*, 46, 1048–1053.

Reed, P.B., Peterson, M.L., Pfeifer-Meister, L.E., Morris, W.F., Doak, D.F., Roy, B.A. et al. (2021) Climate manipulations differentially affect plant population dynamics within versus beyond northern range limits. *Journal of Ecology*, 109, 664–675.

Rees, M. & Ellner, S.P. (2009) Integral projection models for populations in temporally varying environments. *Ecological Monographs*, 79, 575–594.

Rozendaal, D.M.A., Phillips, O.L., Lewis, S.L., Affum-Baffoe, K., Alvarez-Davila, E., Andrade, A. et al. (2020) Competition influences tree growth, but not mortality, across environmental gradients in Amazonia and tropical Africa. *Ecology*, 101, e03052.

Schultz, E.L., Hülsmann, L., Pillet, M.D., Hartig, F., Breshears, D.D., Record, S. et al. (2022) Climate-driven, but dynamic and complex? A reconciliation of competing hypotheses for species' distributions. *Ecology Letters*, 25, 38–51.

Seager, R. & Vecchi, G.A. (2010) Greenhouse warming and the 21st century hydroclimate of southwestern North America. *Proceedings of the National Academy of Sciences*, 107, 21277–21282.

Sheth, S.N. & Angert, A.L. (2018) Demographic compensation does not rescue populations at a trailing range edge. *Proceedings of the National Academy of Sciences*, 115, 2413–2418.

Shirk, A.J., Cushman, S.A., Waring, K.M., Wehenkel, C.A., Leal-Sáenz, A., Toney, C. et al. (2018) Southwestern white pine (*Pinus strobiformis*) species distribution models project a large range shift and contraction due to regional climatic changes. *Forest Ecology and Management*, 411, 176–186.

Shriver, R.K., Yackulic, C.B., Bell, D.M. & Bradford, J.B. (2021) Quantifying the demographic vulnerabilities of dry woodlands to climate and competition using range-wide monitoring data. *Ecology*, 102, e03425.

Stanke, H., Finley, A.O., Domke, G.M., Weed, A.S. & MacFarlane, D.W. (2021) Over half of western United States' most abundant tree species in decline. *Nature Communications*, 12, 451.

Talluto, M.V., Boulangeat, I., Vissault, S., Thuiller, W. & Gravel, D. (2017) Extinction debt and colonization credit delay range shifts of eastern North American trees. *Nature Ecology & Evolution*, 1, 0182.

Tingley, M.W., Monahan, W.B., Beissinger, S.R. & Moritz, C. (2009) Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences*, 106, 19637–19643.

Tredennick, A.T., Teller, B.J., Adler, P.B., Hooker, G. & Ellner, S.P. (2018) Size-by-environment interactions: a neglected dimension of species' responses to environmental variation. *Ecology Letters*, 21, 1757–1770.

Turner, M.G., Braziunas, K.H., Hansen, W.D. & Harvey, B.J. (2019) Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. *Proceedings of the National Academy of Sciences*, 116, 11319–11328.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z. et al. (2009) Widespread increase of tree mortality rates in the western United States. *Science*, 323, 521–524.

Villellas, J., Doak, D.F., García, M.B. & Morris, W.F. (2015) Demographic compensation among populations: what is it, how does it arise and what are its implications? *Ecology Letters*, 18, 1139–1152.

Wang, T., Hamann, A., Spittlehouse, D. & Carroll, C. (2016) Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS One*, 11, e0156720.

Wang, X., Piao, S., Ciais, P., Li, J., Friedlingstein, P., Koven, C. et al. (2011) Spring temperature change and its implication in the change of vegetation growth in North America from 1982 to 2006. *Proceedings of the National Academy of Sciences*, 108, 1240–1245.
Woodall, C.W., Oswalt, C.M., Westfall, J.A., Perry, C.H., Nelson, M.D. & Finley, A.O. (2009) An indicator of tree migration in forests of the eastern United States. *Forest Ecology and Management*, 257, 1434–1444.
Yang, X., Li, S., Shen, B., Wu, Y., Sun, S., Liu, R. et al. (2018) Demographic strategies of a dominant tree species in response to logging in a degraded subtropical forest in Southeast China. *Annals of Forest Science*, 75, 84.
Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M. et al. (2020) Forest microclimate dynamics drive plant responses to warming. *Science*, 368, 772–775.
Zhang, J., Huang, S. & He, F. (2015) Half-century evidence from western Canada shows forest dynamics are primarily driven by competition followed by climate. *Proceedings of the National Academy of Sciences*, 112, 4009–4014.
Zhu, K., Woodall, C.W. & Clark, J.S. (2012) Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology*, 18(3), 1042–1052.
Zimmermann, N.E., Yoccoz, N.G., Edwards, T.C., Meier, E.S., Thuiller, W., Guisan, A. et al. (2009) Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences*, 106, 19723–19728.
Zuidema, P.A. & Franco, M. (2001) Integrating vital rate variability into perturbation analysis: an evaluation for matrix population models of six plant species. *Journal of Ecology*, 89, 995–1005.

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