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Climate-driven, but dynamic and complex? A reconciliation of competing hypotheses for species' distributions

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Abstract

Estimates of the percentage of species "committed to extinction" by climate change range from 15% to 37%. The question is whether factors other than climate need to be included in models predicting species' range change. We created demographic range models that include climate vs. climate-plus-competition, evaluating their influence on the geographic distribution of *Pinus edulis*, a pine endemic to the semiarid southwestern U.S. Analyses of data on 23,426 trees in 1941 forest inventory plots support the inclusion of competition in range models. However, climate and competition together only partially explain this species' distribution. Instead, the evidence suggests that climate affects other range-limiting processes, including landscape-scale, spatial processes such as disturbances and antagonistic biotic interactions. Complex effects of climate on species distributions—through indirect effects, interactions, and feedbacks—are likely to cause sudden changes in abundance and distribution that are not predictable from a climate-only perspective.

KEYWORDS
climate, competition, complex systems, demography, disturbances, forest inventory, integral projection model, range limits, scale, species distributions

INTRODUCTION

Climate has long been viewed as an essential determinant of species' geographic distributions. Ecologists therefore expect that anthropogenic climate change (IPCC 2013; Le Quéré, 2018) will change species' distributions and ultimately drive some species to extinction (Chen et al., 2011; Parmesan & Yohe, 2003; Thomas et al.,

2004). Static climate envelope models (also called species distribution models) rely heavily on this view and are widely used to project future species distributions and make planning decisions to prevent extinction (Chen et al., 2011; Parmesan & Yohe, 2003; Thomas et al., 2004).

At the same time, ecologists recognise potential limitations of these models. One concern is whether additional factors need to be considered, beyond climate,

to understand or predict species' distributions. Long-standing hypotheses about the causes of range limits, beginning with Darwin (Brown, 1995; Darwin, 1859; Dobzhansky, 1950; MacArthur, 1972; and others), propose that biotic interactions should be important, particularly where abiotic conditions are benign (e.g., in the tropics). Hence, species' distributions may be limited by climate, by biotic interactions, or species may sort along gradients of opposing forms of stress according to evolutionary trade-offs, such that climate is limiting at one range edge and competition at another (Austin, 1990; Barton, 1993; Ettinger et al., 2011; Guisan & Zimmerman, 2000; Louthan et al., 2015; Sexton et al., 2009). Indeed, Hutchinson (Hutchinson, 1957, 1978) highlighted the importance of biotic interactions by distinguishing between the fundamental vs. realised ecological niche, pointing out that competitive biotic interactions can exclude species from their fundamental climatic niche (Connell, 1961; Louthan et al., 2015). While the existence of these biotic interactions at a small scale is undisputed, some have argued that they are inconsequential at the scale of geographic distributions (Copenhaver-Parry et al., 2017; Gotelli et al., 2010; McGill, 2010). A few recent studies have provided evidence that biotic interactions are important in shaping distributions (Belmaker, 2015; Gotelli et al., 2010; Grady et al., 2019), but comparative studies and reviews have found more evidence for climatic or biophysical limits on ranges (Brown et al., 1996; Sexton et al., 2009). Ecologists are thus faced with the expectation, from first principles, that biotic interactions *should* be important, contrasting with sparse evidence that they are. Successful prediction of species' future distributions depends on understanding the governing drivers, and at present, our understanding is still limited.

A second concern is that static climate envelope models presume that the conditions needed to support a species can be inferred from occurrence data, when in fact species can be absent from suitable habitat because of dispersal limitation (Davis & Shaw, 2001; Meier et al., 2012; Pagel et al., 2020; Soberón, 2007) and present in unsuitable habitat because of source-sink dynamics (Pulliam, 2000). Thus the use of occurrence data to infer the niche and predict distribution may be misleading, including attempts to account for biotic interactions using joint species distribution modelling (Pichler & Hartig, 2020; Record et al., 2018; Warton, 2015). To address this problem, the case has been made for a demographic approach to range modelling (Ehrlén & Morris, 2015; Huntley et al., 2010; Normand et al., 2014; Pagel & Schurr, 2012; Schurr, 2012), which determines the conditions under which population growth rate is expected to be at or above the replacement level of 1.0, "permitting the species to exist indefinitely" (Holt, 2009; Hutchinson, 1957, 1978; Peterson, 2011). That is, a demographic approach is distinguished by analysis of vital rates rather than occurrence data to determine the suitability—i.e., survival, growth, and fertility. By combining vital rate responses to environmental variation together in a population model, it is possible to project where populations are expected to decline, increase, or be stable, and the species to therefore be present or absent (Figure 1). There are few examples of demographic range modelling (Diez et al., 2014; Merow et al., 2011, 2014; Pagel et al., 2020; Pironon, 2017), and none, to our knowledge, have included effects of competition (though see dynamic vegetation models; Snell et al., 2014).

Here we evaluate how climate and competition influence the demography and hence the expected geographic distribution of a tree species. We test two alternative hypotheses, which we refer to as hypothesis C1 (climate-only) and hypothesis C2 (climate-plus-competition). We focused on a tree species because extensive demographic data can be derived from national forest inventories. Specifically, the study organism is *Pinus edulis* (Engelm.), two-needle or Colorado piñon, a small-statured pine endemic to the semiarid Colorado Plateau in the southwestern U. S. This species may serve as a leading indicator of climatically driven change in the distribution of forest ecosystems because of its position at the arid edge of the forest biome and its documented sensitivity to climate (Adams, 2009; Allen & Breshears, 1998; Breshears, 2009; Breshears et al., 2018; Clifford et al., 2013; Williams, 2013). Because the elevation is recognised by ecologists as an important gradient that organises abiotic and biotic features of the environment (Daubenmire, 1943; Merriam, 1890; Shreve, 1922; Whittaker, 1967), climate and competition were evaluated as factors limiting *P. edulis* across elevation.

Our analysis follows three lines of evidence. First, we evaluated the response of vital rates to environmental gradients (Figure 1, Step 1). Hypotheses C1 and C2 lead to contrasting predictions about how vital rates should vary across environmental gradients (Figure 2a–c). If climate limits both edges of the geographic distribution (hypothesis C1), vital rates should decline at the margins of the species' climatic range. This could be in response to a single limiting climate variable (dashed orange lines, Figure 2a, b), or in response to more than one limiting climate variable (solid orange lines, Figure 2a, b). For example, if temperature alone is responsible for range limits through its effect on one or more vital rates, there should be a unimodal response to temperature variation with elevation (dashed orange line, Figure 2b). Alternatively, precipitation may limit one or more vital rate at the low-elevation, dry edge of *P. edulis*' range (solid orange line, Figure 2a) whereas temperature may be limiting at the high-elevation, cold edge of *P. edulis*' range (solid orange line, Figure 2b). In addition, under hypothesis C1, vital rates should be unresponsive to competition (solid orange line, Figure 2c). Under hypothesis C2, vital rates should decline with climate at one edge and with competitive pressure at another edge (green, Figure 2a–c). We do not evaluate the hypothesis that biotic interactions limit both edges of *P. edulis*' distribution because
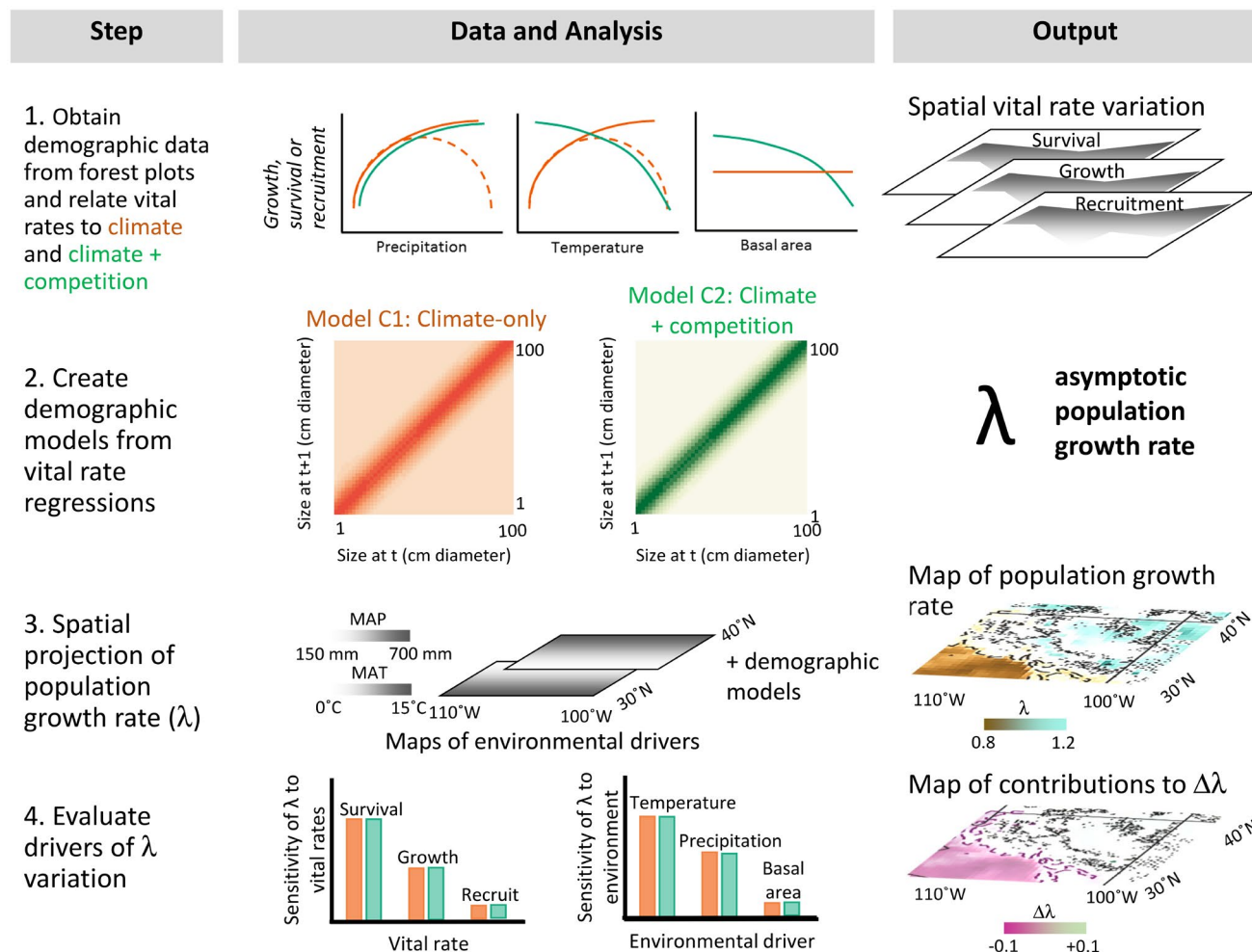
FIGURE 1 Simplified representation of the pipeline of analysis, showing the types of data and analysis used for each step and the outcome of each step. Step 1, vital rate modelling with generalised additive models (i.e., the influence of environmental drivers on vital rate variation); Step 2, combination of vital rate models into a demographic model, here shown as a heat map of the probability distribution of tree size at time t+1, conditional on its size at time t and its survival to time t+1, to predict the asymptotic population growth rate; Step 3 spatial projection asymptotic population growth rate (λ) from the demographic model and maps of climate or climate and competition—where predicted λ is at or above the replacement level of 1.0, population persistence is expected, and the species is expected to be present rather than absent.; and, Step 4, perturbation analyses of the influence of vital rates and environmental drivers on λ

its lower-elevation distribution limit marks the climatic (arid) limit of the tree growth form and the forest biome. We tested these hypotheses using observations on >20,000 trees sampled in almost 2000 forest inventory plots using vital rate models of growth, mortality, and recruitment as a function of climatic factors alone (hypothesis C1) vs. climate in combination with the competition proxy basal area (hypothesis C2).

Second, we evaluated the fit of two demographic range models (DRMs), reflecting hypotheses C1 vs. C2, to *P. edulis* occurrence data. That is, we combined the statistical vital rate models (survival, growth, and fertility) for C1 and C2 described above into a population model known as an integral projection model (IPM), and from the IPM, created maps of *P. edulis'* expected population growth rate (λ), using maps of climate (hypothesis C1) or climate and competition (hypothesis C2; Figure 1, Steps 2 and 3). The expectation is that the probability

of occurrence of *P. edulis* should increase with DRM-predicted λ, and in particular, that a high probability of occurrence is expected where predicted $\lambda \geq 1.0$, the threshold above which individuals replace themselves on average and hence populations should persist. With this analysis we ask, do demographic predictions based on hypothesis C1 or C2 better match *P. edulis'* observed distribution?

Third, we used perturbation analyses (Caswell, 2001) to probe the causes of range limits. Perturbation analyses examine the effect of small changes in vital rates or environmental drivers on λ. These analyses showed which vital rates have the greatest proportional influence on λ, and which vital rates and underlying environmental drivers contribute the most to areas of mismatch between predicted population growth rate and observed geographic distribution (Figure 1, Step 4). This combination of demographic analyses—vital rate responses inferred from
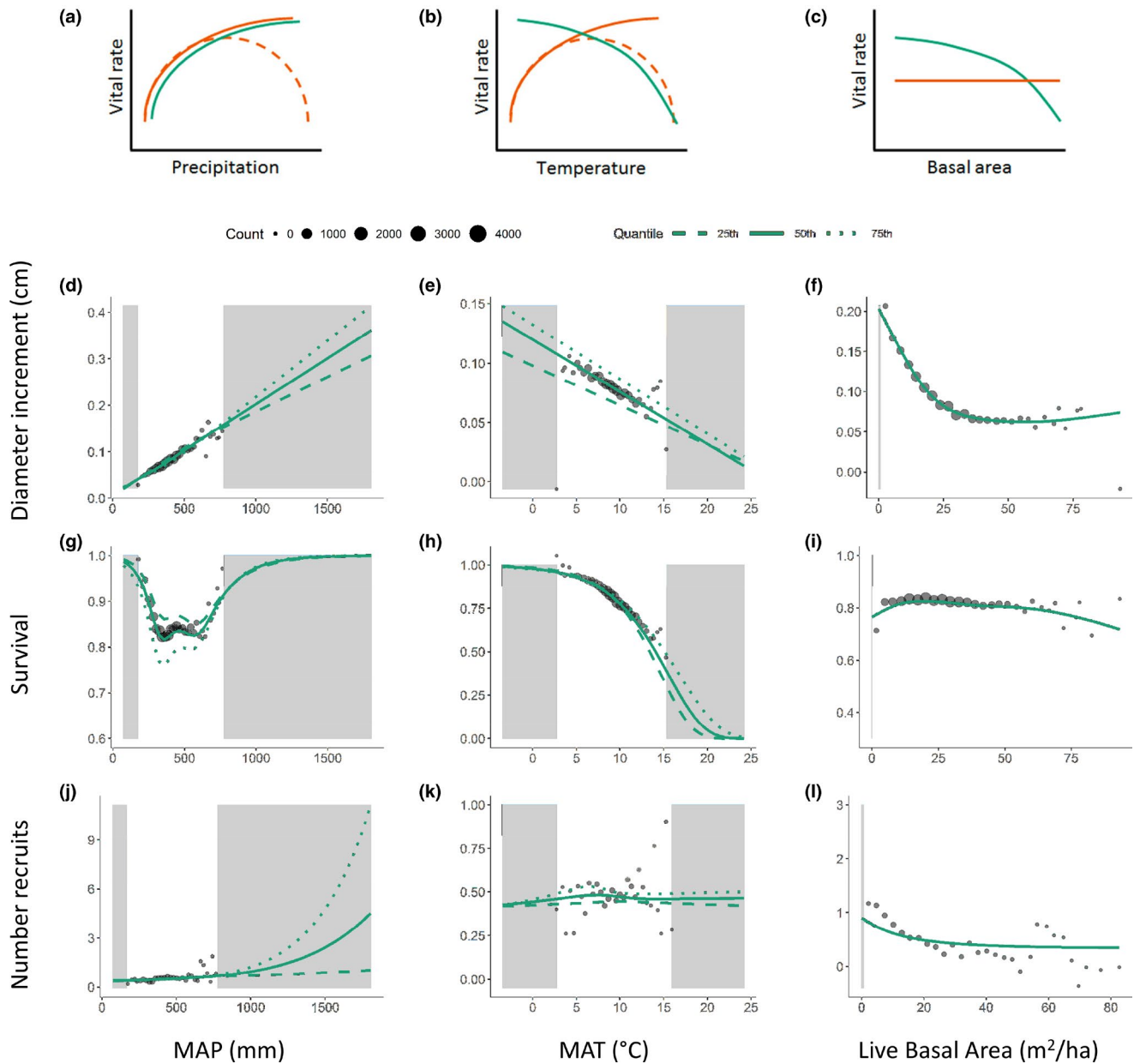
FIGURE 2 Responses of *Pinus edulis* vital rates to climate and competition. (a–c) Predicted responses to gradients of precipitation, temperature, and tree basal area under hypothesis C1 (orange; climate limits both range edges) vs. C2 (green; climate and competition each limit one range edge). Under hypothesis C1, just one vs. more than one climate variable might be limiting (dashed vs. solid orange lines, respectively). Panels (d–l) shows the inferred response of individual tree growth (d–f), survival (g–i), and the rate of recruitment of new trees (j–l) to mean cumulative annual precipitation (MAP), mean annual temperature (MAT), and basal area of all live trees per forest inventory plot. Comparisons between predicted (a–c) and inferred (d–l) vital rate responses can thus be made within each column. Inferred response curves in panels (d–l) are shown across the full range of environmental conditions observed in the study domain. Those conditions *not* occupied by *P. edulis* are shaded grey. Responses to MAP and MAT are shown for the 25th (dashed line), 50th (solid line), and 75th (dotted line) percentiles of the other climate variable, illustrating MAT-MAP interactions. Binned averages of the data are overplotted on the model-inferred response, with symbol size indicating the number of trees per bin

thousands of individuals and locations, the formation of a structured population model that includes the effects of climate and competition, and perturbation analyses of that demographic model—allowed us to test two classic hypotheses for the causes of range limits in a novel and rigorous way. This is the first hypothesis-driven test of process-based distribution models that we are aware of, and the first time that a demography-based model of a

species' distribution has been used to decompose the influences of climate and competition on model-predicted performance. Based on our results, we suggest how the two hypotheses may be reconciled to form a more complex and dynamic explanation for species distributions that is consistent with the data. Finally, we indicate the implications of this updated hypothesis. While climate is a dominant and overarching influence on species

geographic distributions, it is likely that climate-only models will fail to capture range dynamics, particularly in cases where climate has both direct and indirect effects on vital rates, the latter involving additional range-limiting processes. Climate-driven but complex transient range dynamics, including sudden changes in abundance and distribution, may lead the loss of biodiversity to be much greater than what is predicted from static, climate-only models.

MATERIALS AND METHODS

Demographic, climate, and competition data

We derived demographic data on *P. edulis*—including tree survival, growth, and recruitment—from the U.S.D.A. Forest Service's Forest Inventory Analysis database (see *forest inventory data*, Appendix S1), leading to 23,069 records of survival and 18,122 records of diameter growth. Counts of new trees that reached the minimum size threshold of 2.54 cm were obtained from 1872 plots where *P. edulis* was present.

These vital rates—survival, growth, and recruitment—were predicted as a function of climate-only (hypothesis C1) or climate and competition (hypothesis C2; step 1 in Figure 1). Historical climate data were extracted from the PRISM Climate Group web archive (http://prism.oregonstate.edu/, data set AN81m, 4-km resolution), including monthly temperature, vapour pressure deficit (VPD), and precipitation, as well as 1981–2010 climate normals. A list of the 72 climate variables tested in vital rate models is found in Table S1 (Appendix S1).

Across the study domain, temperature declines and precipitation increases with increasing elevation (Figure S1a, b, see Appendix S1). With more precipitation, the basal area of living trees increases (Figure S1c in Appendix S1). We used the latter, the basal area of living trees (all species) on a plot (BALIVE; from the FIA Condition Table), as a proxy for the combined effect of inter- and intra-specific competition for light. Soil moisture is another important limiting factor across the study domain, but because both supply (precipitation) and demand (basal area of live trees) increase with elevation, it is difficult to say whether basal area is a good proxy for soil moisture competition.

Fitting demographic range models

We created demographic range models (DRMs) by first creating statistical models of how vital rates respond to environmental drivers (step 1 in Figure 1). These vital rate models were then combined together to create integral projection models (IPMs; step 2 in Figure 1). An IPM consists of a kernel, a function that maps the state (e.g., size) of an individual in the present to its state (along with those of offspring) in the next time step. The IPM kernel is based on estimates of vital rates (survival, growth, and reproduction) as a function of at least one continuous state variable (Easterling et al., 2000; Ellner et al., 2016; Ellner & Rees, 2006)—here, tree size, measured as the diameter at root collar—and potentially other predictors (i.e., the environmental drivers). See detailed methods in Appendix S1 under *integral projection model*. These IPMs were constructed using either climate-only models of vital rates (hypothesis C1) or vital rate models that included climate and competition as predictors (hypothesis C2), both with interactions between the climate variables. Other examples of environmentally sensitive IPMs include Coulson et al. (2011) and Simmonds et al. (2020).

We used generalised additive models (GAMs) to predict vital rates as a function of covariates (step 1 in Figure 1), as in Ozgul et al. (2010), with plot as a random effect influencing the model intercept to capture site-level variation in vital rates caused by unidentified factors (e.g., soil characteristics). GAMs were chosen because they can be fit flexibly to data, with extrapolation based on the response at the edge of the data, rather than imposed by a particular functional form (Harrell, 2015). The one exception to this was the response of survival to temperature, which extrapolated poorly under a GAM, and instead had a reasonable response using a linear model without a quadratic term (see additional detail in *vital rate models*, Appendix S1).

To decide which climate variables should enter vital rate models, we used a forward stepwise approach guided by Akaike's Information Criterion (AIC). We first selected between 30-year normals of mean annual climate variables vs. mean annual climate specific to the census interval. We then substituted in 3 or 4 seasonal variables, and finally added climate anomalies. Climate normals of mean annual precipitation and temperature were the best predictors of variation in growth, likely a result of the coarse temporal resolution of forest inventory data (i.e., growth is measured at ~10-year intervals). Seasonal variables were better predictors of survival and recruitment (ΔAIC of 21 and 52, for survival and recruitment, respectively), but these more complex models also resulted in large uncertainty where data were sparse (Figure S5), hence we chose to use 30-year normals of mean annual precipitation and temperature as covariates in all three vital rate models, to avoid overfitting (see additional detail in *vital rate models*, Appendix S1).

Geographic range projections

We created maps of expected population growth rate based on the two DRMs described above (C1 vs. C2) and maps of climate and competition covariates (step 3 in Figure 1). Climate normals (monthly average

temperature and monthly precipitation) were extracted from PRISM, then rescaled to 16-km resolution. Monthly values were summed or averaged to form mean annual precipitation and temperature, respectively. We created a raster of tree basal area using a random forest model trained with basal area observations from all FIA plots in the study domain as well as climate predictors (mean annual temperature and precipitation) and spatial coordinates (see under *basal area map* in Appendix S1). IPM kernels were then constructed for each grid cell on the landscape by forcing vital rate models with grid cell-specific climate data only (hypothesis C1) or climate and competition data (hypothesis C2). The asymptotic population growth rate, λ, was derived as the dominant eigenvalue of the discretised IPM. We used bootstrapping to estimate 95% confidence intervals for λ (see *integral projection model* in Appendix S1). This analysis answers the question—what is the expected asymptotic population growth rate, given certain hypotheses (C1 vs. C2)?—indicating whether the population is expected to decline, be stable, or increase, under specified, static conditions of climate and the basal area of live trees.

Comparison of DRM-predicted vs. observed distribution

We used logistic regression with a cloglog link function to test the ability of λ from DRMs (C1 vs. C2) to predict the observed probability of presence of *P. edulis* in FIA plots. Occurrence of *P. edulis* should increase with increasing DRM-predicted λ. Deviance from these logistic regressions was used to compare the performance of DRMs C1 vs. C2. While DRM C2 is slightly more complex than C1, the presence-absence validation data are independent of the data used for fitting the vital rate models, so there is no need to adjust for complexity in this model comparison. We also plotted residuals from the logistic regressions against each underlying driver (climate and competition) to examine the environmental conditions under which the fit between DRM-predicted λ and occurrence is poorest.

Perturbation analyses

We used perturbation analyses to examine which vital rates and environmental drivers are responsible for changes in λ across environmental gradients and across space (step 4 in Figure 1). First, we used elasticity analysis (Caswell, 2001) to assess the proportional sensitivity of λ to changes in survival-growth vs. recruitment across elevation—i.e., using average climate and competition values associated with elevation. We then used a life table response experiment (Caswell, 2001) to decompose variation in λ across the landscape into the

contributions of the three vital rates and three drivers of those vital rates. The first step was the calculation of λ under the average environmental conditions where *P. edulis* is present (λ_{ave}). We then found the difference in λ between each grid cell on the landscape ($\lambda_{cell.i}$) and λ_{ave}, denoted $\Delta\lambda_i (= \lambda_{cell.i} - \lambda_{ave})$. Following the methods of Caswell (2001) for a categorical life table response experiment, we then decomposed $\Delta\lambda_i$ into the contribution made by each vital rate, which is determined by a) the difference between the value of the vital rate under the average conditions where *P. edulis* is present vs. its value in that cell and b) the sensitivity of λ to that vital rate. This same approach was used to decompose $\Delta\lambda_i$ into the contributions of each environmental driver (temperature, precipitation, and basal area). See *Perturbation analyses* in Appendix S1.

Because the DRMs predicted λ greater than the replacement value of $\lambda = 1.0$ at high elevations, we ran an additional perturbation analysis to determine how much growth vs. survival vs. recruitment would have to decline for λ to be <1.0 at the observed upper-elevation limit of *P. edulis*. We used expected values of temperature, precipitation, and basal area at the upper-elevation limit to calculate expected vital rates. We then decreased each vital rate from 100 to 0 percent and recalculated λ for each level of perturbation.

Analyses were conducted in R v. 3.6.1 (R Core Team, 2019). Scripts are available through GitHub at https://github.com/emilylschultz/DemographicRangeModel.

RESULTS

Vital rate responses to climate and competition

Responses of *P. edulis* vital rates to competition and climate followed the predictions of hypothesis C2 (green in Figure 2a–c). Growth and recruitment increase in response to more precipitation (Figure 2d, j), and growth and survival decline in response to warmer temperatures (Figure 2e, h). Since temperature declines and precipitation increases with increasing elevation, this indicates climate is stressful at low elevations and benign at high elevations both with respect to temperature and precipitation. These climate effects were consistent between climate-only vs. climate-plus-competition models (compare Figure 2 to Figure S6). In addition, greater basal area of live trees reduced tree-level growth (Figure 2f) and, to a lesser degree, recruitment of new trees (Figure 2l), consistent with negative effects of competition. The surprising increase of survival at both lowest and highest values of mean annual precipitation (Figure 2g) could be the effect of a confounding variable not included in survival models, or it might be caused by local evolution of longevity associated with extreme drought-tolerance at the low-elevation, dry limit of *P. edulis*' distribution, combined with benign precipitation

conditions at the upper-elevation, mesic limit (see *vital rate models* in Appendix S1).

Fit of demographic range models to occurrence data

Population growth rate (λ) predicted by the climate-plus-competition (C2) DRM fit the data on *P. edulis'* occurrence in forest inventory plots better than λ from the climate-only DRM, improving the log likelihood by ~190 units (Figure 3a vs. b). Both DRMs do well in terms of predicting a low population growth rate (λ) where the probability of *P. edulis'* presence is low (Figure 3a, b), which corresponds to warm, dry parts of the study domain below 1000 m (Figure 4a, b). In this same (warm-arid) environmental space, residuals of the logistic regressions are small, indicating a good fit of λ to occurrence data (Figure 3c, d). The predictive performance of both DRMs is poorest in regions with high precipitation (Figure 3c), low temperature (Figure 3d), and at highest values of predicted λ (Figure 3a, b). Both DRMs predict a population growth rate that increases with elevation, rapidly at first, then reaching a plateau slightly above the replacement value of 1.0 (Figure 4d and Figure S7d).

Perturbation analyses

Elasticity analysis showed that the survival-growth sub-kernel has by far the greatest influence on λ across all elevations (Figure S8a), as expected for a long-lived species. The life table response experiment further revealed that survival (not growth or recruitment) is chiefly responsible for low predicted λ below 1000 m (pink in Figure 5a). This is caused by higher temperatures, which make a strong negative contribution to predicted λ below 1000 m (pink in Figure 5b). Survival is also responsible for higher-than-average predicted population growth rates (green in Figure 5a). High survival is driven by low temperature and high precipitation, which make the greatest positive contributions to $\Delta\lambda_i$ (Figure 5b). At high elevation, where the fit of the DRM to occurrence data deteriorates, recruitment would have to decline by 50% for λ to be equal to the replacement rate of 1.0, but survival would only have to decline by 2% (Figure S8b, c).

DISCUSSION

Demographic analyses revealed greater support for the hypothesis that both climate and competition influence
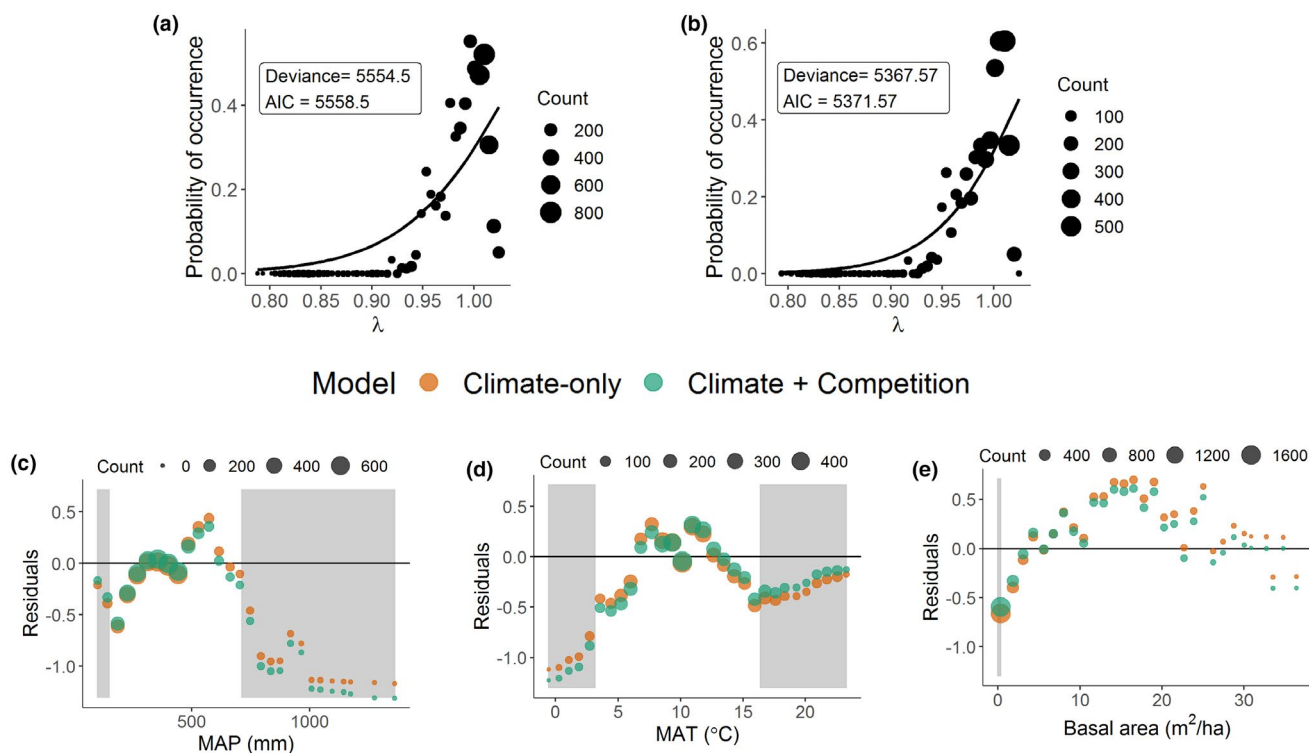

FIGURE 3 Validation of the two demographic range models (DRMs) of *Pinus edulis* to presence-absence data. (a and b) Probability of occurrence in forest inventory (FIA) plots, as a function of population growth rates (λ) from climate-only (a) and climate-plus-competition (b) DRMs, fit by a logistic regression. (c–e) Deviance residuals of the logistic regressions in panels (a and b), as a function of mean annual precipitation (c), mean annual temperature (d), and tree basal area (e). Smaller absolute residuals indicate a better fit of model predictions to observed occurrence. Residuals in panels (c–e) are shown across the full range of environmental conditions observed in the study domain, illustrating the fit of model predictions extrapolated beyond the range of conditions occupied by *P. edulis* (grey shading)
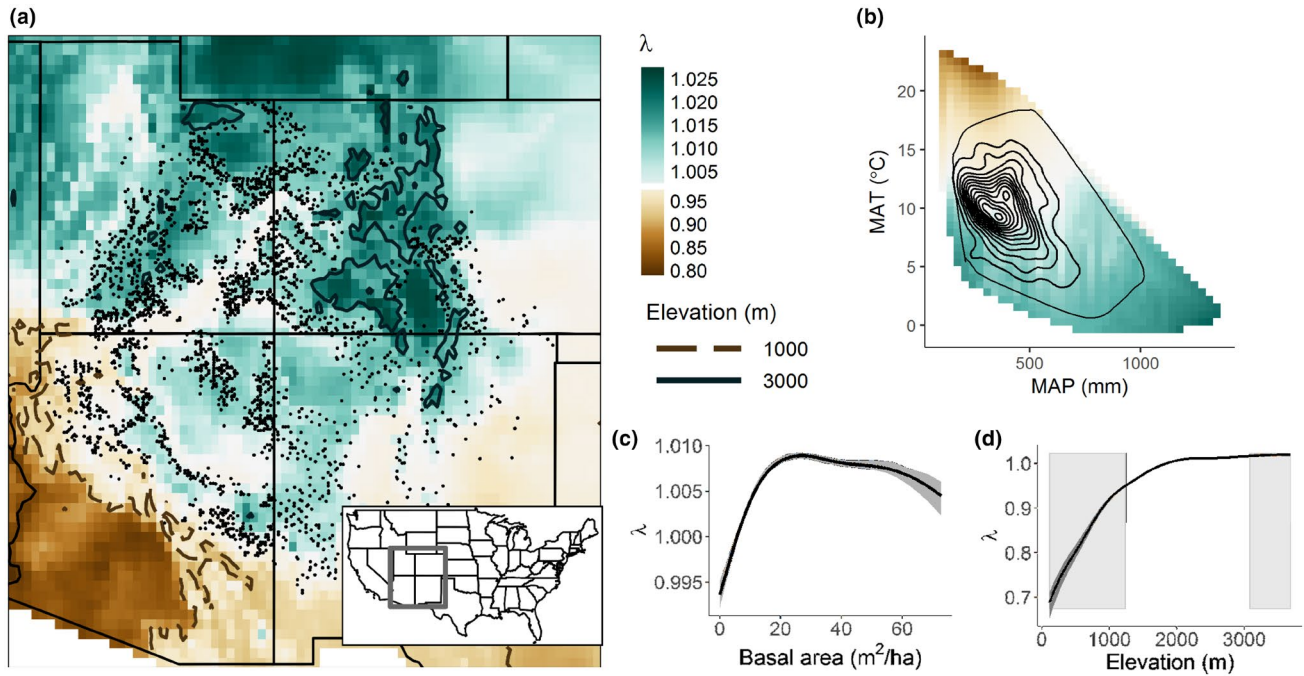
FIGURE 4 Population growth rate (λ) of *Pinus edulis*, from a demographic range model (DRM) including both climate and competition as predictors (hypothesis C2). (a) Map of λ, with points showing the location of forest inventory plots where *P. edulis* is present. Note that changes in λ are an order of magnitude smaller at high elevation than at low elevation, hence the colour scale above the replacement value of 1.0 is greatly expanded compared to the scale below 1.0. (b) Distribution of λ in climate space (mean annual temperature vs. mean annual precipitation), with contours showing the frequency of FIA plots containing *P. edulis*. (c and d) λ as a function of basal area of trees (c) and elevation (d). For comparison with the climate-only model, see Figure S7

the distribution (C2). First, vital rate responses matched the predictions from hypothesis C2 (green in Figure 2a–c) rather than hypothesis C1. Vital rates are negatively impacted by warm-dry conditions at low elevation and by competition at cool-mesic, high-elevation sites, indicating that climate and competition form opposing gradients of stress with elevation. Second, the population growth rate predicted by the climate-plus-competition DRM had a better fit to *P. edulis* presence-absence data in forest inventory plots.

Though the difference in fit to presence-absence data between the two demographic range models is substantial ($\Delta AIC \sim 190$), the patterns of fit are similar (Figure 3). For both DRMs, the fit is best at low values of λ and worst at high values of λ (Figure 3a, b). Perturbation analyses identified that low values of λ are caused by low predicted survival (Figure 5a), which in turn is caused by high average temperature (Figure 5b). This indicates that climate limits population growth rate at the low-elevation, warm and dry edge of *P. edulis*' distribution through temperature-driven mortality. In fact, our range-wide demographic analysis predicts considerable range retraction from this edge of *P. edulis*' distribution, based on data spanning the pulse of *P. edulis* mortality in the early 2000's attributed to warm drought: the model indicates λ below the replacement level of 1.0 up to an elevation of approximately 1800 m, more than 300 m above the current lower-elevation limit of *P. edulis*' distribution (Figure 4d), consistent with other studies documenting

or predicting climate-induced range change in *P. edulis* (Adams et al., 2009; Allen & Breshears, 1998; Breshears et al., 2009; Clifford et al., 2013; Williams et al., 2013). Warming temperatures (U.S. Global Change Research Program et al., 2017) are already impacting this species' distribution.

However, no upper-elevation range boundary is predicted by the DRMs: λ only increases with elevation, never returning below the replacement level of 1.0, even after *P. edulis*' observed upper-elevation limit is reached (grey shading, Figure 4d). Both DRMs predict high λ in high-elevation, cool-mesic locations where *P. edulis* is in fact absent (Figure 4a and Figure S7a). This adds to a growing body of evidence of mismatches between predicted demographic performance and observed occurrence (Bohner & Diez, 2020; McGill, 2012; Pagel et al., 2020; Thuiller, 2014). Ours is the first study in which perturbation analyses offer an explanation for this mismatch. The life table response experiment showed that survival is responsible for high predicted values of λ (Figure 5a), driven by lower average temperatures and higher average precipitation (Figure 5b), with negligible contribution from the competition. This is because competition negatively affects two vital rates with little impact on λ, individual tree-level growth and recruitment (Figure 2f and l), and does not affect survival (Figure 2i), the vital rate with the greatest impact on λ. The finding that competition is not a detectable agent of mortality
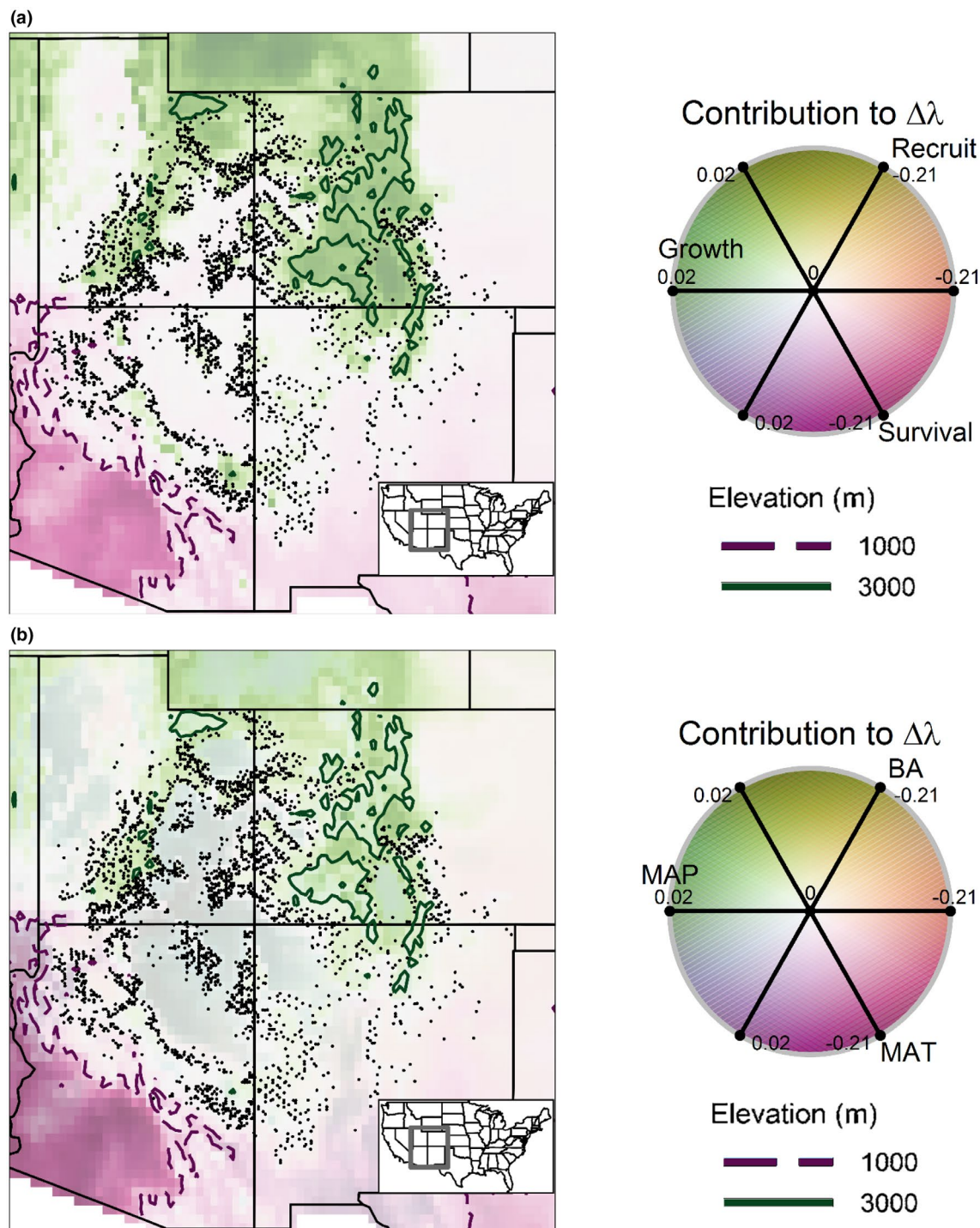
FIGURE 5 Decomposition of differences in population growth rate (λ) of *Pinus edulis*, from a life table response experiment. In both panels, $\Delta\lambda_i$ is $\lambda_{cell.i} - \lambda_{ave}$, the difference in λ predicted for each grid cell ($\lambda_{cell.i}$) compared to λ predicted under the average climate and competition conditions where *P. edulis* is found (λ_{ave}). Colour indicates the contribution of (a) three vital rates and (b) three environmental predictors to $\Delta\lambda_i$, using three divergent colour scales centred on zero and overplotted with transparency. The absolute value on each scale indicates the magnitude of the influence of a vital rate or environmental predictor on $\Delta\lambda_i$, with negative values indicating that a vital rate or environmental predictor causes $\lambda_{cell.i}$ to be smaller than λ_{ave}. Note that the colour scales have asymmetric limits

in *P. edulis* is corroborated by a recent review of 21 studies of mortality in this species, covering a wide range of methodologies and scales (Meddens, 2015). As a consequence, the negative effect of increasing competition, while detectable, is weak compared to

the positive effects of temperature and precipitation with increasing elevation, and is insufficient to limit the species' predicted occurrence ($\lambda > 1.0$) at cooler, wetter locations. This adds support to the conclusion of the most recent review of evidence on range limits

(Sexton et al., 2009): climate and competition both have detectable effects, but the effect of competition is weak relative to climate.

If climate and competition are both important factors influencing vital rates, but they do not suffice to explain the distribution of *P. edulis*, how should we understand its geographic distribution? Dispersal limitation is often invoked to explain a species' absence in suitable habitat (Davis & Shaw, 2001; Meier et al., 2012; Pagel et al., 2020; Soberón, 2007), and it could well be the reason for absence of *P. edulis* at a larger scale, i.e., outside the study domain. There is evidence for ongoing northward migration of piñons and other pines in western North America (Cole et al., 2013; Jackson et al., 2005; Kaye et al., 2010). But it is an unconvincing explanation for the absence of *P. edulis* at higher elevations within the study domain, given bird dispersal of piñon seeds and the short distances over which elevation varies in this region.

We propose that the key to understanding *P. edulis'* distribution, and perhaps species distributions more generally, lies in recognising the important grain of truth in the two classic hypotheses. Our results suggest that climate *is* the most important factor determining the distribution of P. edulis, while also indicating that climate

alone *cannot* explain its distribution. It is possible to reconcile these two results with a new hypothesis: climate is such an important driver across scales that it influences other range-limiting processes—including spatial processes such as disturbances and disease—potentially leading to complex range dynamics that are not predictable from a climate-only perspective (Figure 6).

To unpack this hypothesis for species' distributions, we first reconsider the evidence for *P. edulis*, as a case study that illustrates the general mechanisms at work. Because *P. edulis'* population growth rate is most sensitive to survival rate, an additional agent of mortality could do much to explain the mismatch between predicted population growth rate and observed distribution. Indeed, at high elevation, recruitment would have to decline by 50% for λ to be equal to the replacement rate of 1.0, but survival would only have to decline by 2% (Figure S8b, c). Fire could be that missing source of mortality. *Pinus edulis* belongs to the subgenus *Strobus*, a clade of stress-tolerating pines without evolutionary adaptations to fire, contrasting the repeated evolution of fire adaptations in subgenus *Pinus* (He et al., 2012; Keeley, 2012; Keeley & Zedler, 1998; Millar & Richardson, 1998; Pausas, 2015). Forest inventory data
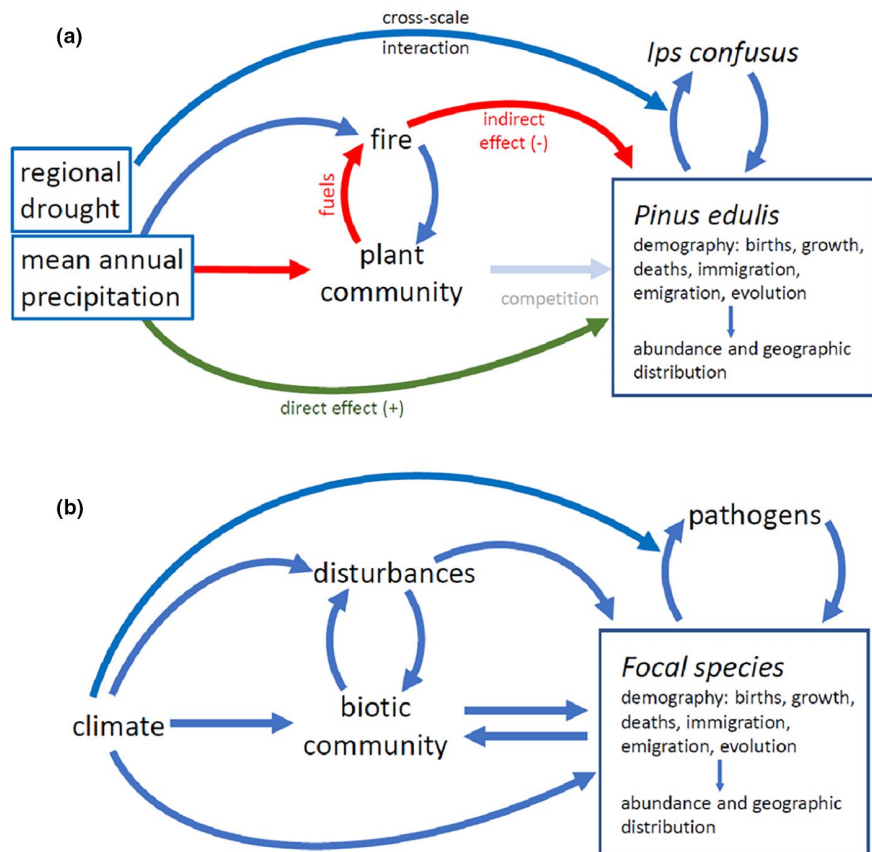

FIGURE 6 Conceptual models of species' distributions. (a) Model of the processes influencing the geographic distribution of *Pinus edulis*, illustrating three key features: (1) positive direct effects of local mean annual precipitation on vital rates (green arrow) vs. negative indirect effect mediated through the feedback between plant community and fire regime (red arrows), (2) weak negative direct effect of competition on *P. edulis*, and (3) cross-scale interaction between acute, regional-scale drought and attack by the bark beetle, *Ips confusus*. (b) A general, conceptual model of the complex effects of climate, biotic community, disturbances, and pathogens on a focal species' geographic distribution

confirm this intolerance of fire: mortality of *P. edulis* exposed to surface and crown fire is high, ~54.9% and ~96.5%, respectively. But forest inventory data further indicate the fire was rare in the period of study (2000–2017), affecting less than 2% of plots and trees (and vital rate models were nearly identical with vs. without these fire-killed trees; Figure S6c, d). Historically, fire would have constrained *P. edulis*' distribution at the ecotone between fire-infrequent piñon-juniper woodlands and fire-frequent *Pinus ponderosa* forest (Allen, 1989, 2007; Swetnam & Baisan, 1996), as well as *P. edulis*' abundance in piñon-juniper savannas (Margolis, 2014). Indeed, the last ~100 years of livestock grazing and fire suppression have led to increases in the abundance and distribution of piñons (Margolis, 2014; Miller & Tausch, 2001; Romme, 2009), consistent with the hypothesis that fire plays a role in limiting *P. edulis*. We suggest that this fire-intolerant species finds refuge from fire on drier parts of the landscape, where productivity of fine fuels is insufficient for fire spread. That is, while the direct effects of precipitation on *P. edulis* vital rates are positive, its indirect effects are negative (Figure 6a), through its influence on the landscape-scale process of fire (Bowman et al., 2015; Staver et al., 2011a, b; Staver & Levin, 2012), tipping the balance between fire-infrequent piñon-juniper woodlands (Romme et al., 2009) and fire-frequent forests and savannas.

The absence of *P. edulis* from wetter parts of the landscape (see grey shading, Figure 2d) could easily have been mistaken for competitive displacement (for example, by a joint species distribution model). That is, on the basis of occurrence data, the replacement of one pine (*P. edulis*) by another (*P. ponderosa*) with increasing mean annual precipitation could have been interpreted as competitive displacement. But our demographic analysis showed that the effect of the competition is negligible on the vital rate that matters most to *P. edulis*' population growth rate (survival), and the direct effects of precipitation on its vital rates are positive. Intolerance of fire, instead, is an explanation for the upper-elevation limit of *P. edulis*' distribution that is consistent with the demographic inference that climatic *and* competitive conditions are suitable there ($\lambda > 1.0$).

Even at the low-elevation limit of *P. edulis*' distribution, which our demographic analysis confirms has the signature of climate limitation, an interaction between climate and another process (insect outbreak) has been identified as a driver of range change (Allen, 2007; McDowell, 2011; Shaw et al., 2005). Regional-scale drought in the early 2000's interacted with attack by the bark beetle *Ips confusus* (Figure 6a), propagating from individual trees to landscape-scale irruption, leading to widespread *P. edulis* mortality (Allen, 2007; McDowell et al., 2011; Shaw et al., 2005). A stochastic analysis of the impact of climate, fire, and insect outbreaks on the expected geographic distribution of *P. edulis* is a critical next step to evaluate the hypothesis that indirect in

addition to direct effects of climate, or cross-scale interactions between climate and other factors are important to be able to describe range dynamics.

The case of *Pinus edulis* illustrates mechanisms that may shape species' distributions more generally (Figure 6b). There are two notable components to this hypothesis for species' distributions. First is that species distributions are influenced by processes at the landscape and macrosystem scales (Franklin, 2010; Heffernan, 2014)—fire, insect outbreaks, and large-scale drought, in the case of *P. edulis*—in addition to the individual, population, and community scales at which niches and distributions have historically been conceived and discussed (Elton, 1927; Grinnell, 1917; Hutchinson, 1957, 1978). Second is the idea that climate is important at all scales and affects other range-limiting processes, operating at a variety of scales. This potentially leads to a complex systems structure, as described by Allen, (2007); Peters, (2004); Peters and Havstad, (2006); Heffernan et al. (2014); Soranno, (2014) for a variety of ecological systems. Under this hypothesis, climate influences species' distributions not only through its direct effects on vital rates, but also through indirect effects, interactions, or feedbacks involving other range-limiting processes (Figure 6b). With changing climate, this has the potential to lead to complex range dynamics, including threshold behaviour that manifests as sudden changes in abundance or distribution. In the example of *P. edulis*, the interaction between large-scale drought stress and an (initially) small-scale, antagonistic biotic interaction (insect attack) led to such threshold behaviour (Allen, 2007; Heffernan et al., 2014)—landscape- and regional-scale irruption, with widespread tree mortality.

This climate-driven, complex systems hypothesis for species' distributions offers a candidate explanation for the rise in mass mortality events (MME's) in certain animals (birds, fishes, and marine invertebrates)—defined as rapidly occurring catastrophic demographic events that punctuate background mortality levels—based on a survey of 727 published examples of such events (Fey, 2015). MME's were frequently attributed to disease and climate (Fey et al., 2015), a combination that can even lead to sudden extinction (e.g., the Monteverde golden toad; Anchukaitis & Evans, 2010). The significance is that while species distributions are strongly determined by climate, range dynamics, especially a species' persistence vs. extinction with climate change, may not be predictable from climate envelope-type models. The task at hand then is to evaluate to what degree or in what organisms this climate-driven, complex systems hypothesis explains dynamic patterns of abundance and distribution. If this hypothesis holds true, we should expect further global weirding of the ecology of planet Earth—sudden changes in species' abundance and distribution—accompanying the weirding of the climate system.

AUTHORSHIP

MEKE, ELS, PZ, FH, and LH designed the research. ELS, MDP, MEKE, and LH contributed new analytic tools (scripts). ELS, MEKE, MDP, and LH analysed the data. MEKE, ELS, PZ, FH, LH, MDP, DDB, SR, RJD, and JDS wrote the paper.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

No new data were used in this work. The scripts for creating a demographic range model from publicly available US Forest Service FIA forest inventory data and PRISM climate data are available in the GitHub repository https://github.com/emilylschultz/DemographicRangeModel.

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SUPPORTING INFORMATION

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