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Population Decline for Plants in the California Floristic Province: Does Demography or Geography Determine Climate Change Vulnerability?

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ABSTRACT

Aim: The role of species' demography and geography can be difficult to disentangle when projecting future population decline under global change. By constructing and combining species-specific ecological models for plants in a fire-prone Mediterranean-type ecosystem, we explored how demography and geography can differentially affect population projections of plant species in the coming century.

Location: California, USA.

Methods: We developed a set of linked demographic-distribution models for six Californian plant species, representing a range of life history characteristics found in the California Floristic Province. These ecological models simulate stochastic population dynamics to show how plant species might differentially respond to geographic patterns in climate change and fire regime scenarios when considering species-specific traits. By integrating each combination of species-specific demographic model with each of the other species' distribution models, we assessed the role of habitat loss and demographic constraints in the population declines of these plants.

Results: We found that all species experienced substantial population decline by 2085 under our simulations, with total species' abundances primarily influenced by habitat loss from climate and land-use change. Species' demography had a larger influence on subpopulation-level dynamics, especially in areas predicted to have frequent wildfires.

Main Conclusions: Our research underscores that responses to climate change are shaped by the interplay between species-specific demography and geographic distribution. Though species distribution models may be able to predict changes in which areas will be suitable throughout species' theoretical niche limits, species-specific population dynamics are critical to projecting how populations might change in abundance at more local scales. Conservation decisions should integrate both geographic and demographic factors to effectively address climate-induced threats at both regional and local scales.

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1 | Introduction

Mediterranean-type ecosystems like the California Floristic Province (CFP) are hotspots for biological diversity (Myers et al. 2000). The CFP has disproportionately high plant diversity, with at least 4300 plant species, 35% of which are endemic, found in a relatively small area of 320,000 km^2 (Cowling et al. 1996). In the coming century, projected changes in climate, fire regimes, and land use put species in these regions at risk of population decline or extinction if plants are unable to adapt to change or disperse beyond their current range (Franklin et al. 2021). Populations of native plant species in this region are already measurably shifting and declining in response to recent climate change (Kelley and Goulden 2008; Rapacciuolo et al. 2014; Wolf et al. 2016; Harrison et al. 2020), with a 19% decline in biomass across California in the last century in part from increased climatic water deficit (McIntyre et al. 2015). These changes, primarily driven by several interacting global change drivers, could result in massive biodiversity loss unless we can better understand and mitigate them (Underwood et al. 2009; Doblas-Miranda 2015).

Among the interacting drivers of plant population decline, temperatures and aridity in the CFP are projected to increase beyond current and historical conditions (Overpeck and Udall 2020). Geographic trends in climate change across the landscape will ultimately determine which areas will be most at risk to plant communities (Ackerly et al. 2010; Rapacciuolo et al. 2014). Climate change will not be uniform in time or space, which will differentially affect species across the landscape depending on their ecological niche (Loarie et al. 2009; Serra-Diaz et al. 2014). Moreover, many Mediterranean-type ecosystems also feature dense human populations, and continuing expansion is likely to exacerbate biodiversity loss (Underwood et al. 2009; Doblas-Miranda et al. 2015); land-use change could be a greater driver of projected habitat loss than climate change (Syphard et al. 2013).

Climate and land-use change are also likely to contribute to changing fire regimes (Keeley and Syphard 2016; Syphard et al. 2019). Within the CFP, decades of fire suppression could cause more fuel-driven wildfires in formerly frequent-fire ecosystems, but in other ecosystems such as coastal shrublands, increased fire frequency associated with population growth and urban expansion is causing the extirpation of species that are adapted to less frequent fire (Syphard et al. 2022). Moreover, trends toward hotter and drier conditions could increase fire probability in some regions (Keeley and Syphard 2016), while land-use change is likely to be more influential than climate in other regions (Syphard et al. 2019). Predicting changes in wildfire frequency throughout the landscape can be difficult and prone to uncertainty (Yang et al. 2015; Syphard et al. 2024); predicting how these changes might affect future plant populations could be even more difficult (Bowman et al. 2020; Coop et al. 2020). Plants in Mediterranean-type ecosystems have adaptations that help them persist in areas with periodic severe fires, and different species are adapted to different fire regimes (Keeley et al. 2011; Pausas and Keeley 2023). For example, oaks and pines with thick bark can resist fire-induced mortality, particularly in low-intensity ground fires (Pausas 2015). The seeds of obligate seeders, such as shrub species in the genera *Ceanothus* and *Arctostaphylos*, germinate only after exposure to heat from wildfire, allowing them to re-establish after fires kill adult populations (Keeley and Zedler 1978). However, these species often need decades after a fire to re-establish a seed bank sufficient to respond to a subsequent fire. Novel fire regimes with frequency or severity beyond historical levels could cause substantial population decline, as plants are adapted to specific fire regimes rather than fire per se (Keeley et al. 2011; Nolan et al. 2021). Thus, plant population decline is a function of how fire regimes are changing and of how species' traits may or may not facilitate resilience.

Modelling and mapping species distributions, range shifts, and habitat loss has been a major focus for understanding how global change could affect future biodiversity across various taxa (e.g., Bellard et al. 2012; Warren et al. 2018). However, these approaches largely ignore important demographic processes that could be critical for understanding the mechanisms of population decline, and they also ignore additional threats that may target demographic processes rather than habitat, such as fire (Thuiller et al. 2014; Swab et al. 2015). In other words, populations may become extinct long before suitable habitat disappears because of interactions among threats and their effects on demographic processes (Brook et al. 2008). One alternative for assessing these interacting effects is to use an integrated modelling framework, combining species distribution models (SDMs) with species-specific population and environmental dynamics (Keith et al. 2008; Franklin et al. 2014; Zurell et al. 2016; Briscoe et al. 2019). This approach has been used for some species (Regan et al. 2012; Conlisk et al. 2012; Syphard et al. 2013; Bonebrake et al. 2014; Backus et al. 2023), but the amount of data necessary to create a biologically feasible model is limited, especially for plants (Crone et al. 2011; Franklin et al. 2017). Even after building and analysing these integrated models, it can be difficult to disentangle whether species-level population dynamics are driven by the geographic trends of the SDM or the ecological trends of the demographic model. More specifically, one could ask whether other species perform similarly under the same distribution models, or whether unique aspects of the species' life history meaningfully contribute to the overall population projections. In short, does it matter more who you are or where you are?

To help disentangle the effects of geography and demography on species' population projections under future global change, we built SDMs and demographic matrix models for six plant species from the CFP (*Ceanothus perplexans*, *C. verrucosus*, *Pinus jeffreyi*, *P. lambertiana*, *Quercus agrifolia*, and *Q. engelmannii*). However, instead of only using species' demographic models with their own distribution model, we factorially combined each combination of distribution and demographic model. These three sets of congeners represent different plant functional types or life history and disturbance response strategies that are widespread among CFP endemic perennial plants—obligate seeding shrubs with lifespans of ~50 years (the *Ceanothus*) with broad (*C. perplexans*) and narrow (*C. verrucosus*) ranges; long-lived conifer trees that are more (*P. jeffreyi*) or less (*P. lambertiana*) fire resistant when large; and long-lived, fire-resistant, and resilient oaks with broad (*Q. agrifolia*) and narrow (*Q. engelmannii*) ranges. These species' demographic models incorporate varying levels of generation time, growth, mortality, fecundity, dispersal, and fire response.

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By comparing the results of each of these species' demographic models linked to each species' distribution models, we were able to ask when population projections depended on geography ('where you are') and when they depended on species-specific traits ('who you are'). Though these models are not meant to represent realistic population projections (even when the same species' population and distribution models are linked), we designed this study to identify conditions under which plant population projections depend on species' geographic and niche limitations and when they depend on demographic characteristics. We expected that the importance of species' demography, climate change geography, and fire dynamics would vary widely between each of the three groups of species. In particular, we expected the fire-dependent, obligate-seeding ceanothus species to depend more on the geography of wildfire dynamics, and the longer-living, fire-resistant species like oaks to be more resilient to shifting climate and fire dynamics.

2 | Methods

2.1 | Overview

To determine how the geography of shifting habitat suitability interacts with species' life-history characteristics among six characteristic plant species from the CFP, we took each species' demographic models and linked them with each SDM (Figure 1). We simulated population dynamics with stage-structured demographic models with stochastic growth, mortality, and fecundity. We used SDMs (detailed in Rose et al. 2023) to estimate changes in habitat quality (converted to local carrying capacities), interpolating between bioclimatic variables in 1995, 2055, and 2085 under two climate models (HadGEM2-ES and CNRM-CM5) and two emissions scenarios (RCP 4.5 and RCP 8.5). To simulate wildfire events, we used a fire distribution model that projects future fire probabilities across California based on historical fire occurrences and climatic and anthropogenic predictors under the four climate models/future scenarios (detailed in Syphard et al. 2024). Using each species' demographic model within each species' distribution model in our experimental design, we differentiated between model results likely the product of species' unique demographic characteristics and those that were the product of the species' geography. If model results were consistent for the same distribution model regardless of demographic model, changes in those populations were likely driven by geography. If there was high variability between demographic models, the unique life history of those species might be more important.

2.2 | Species

We built demographic and distribution models for six fire-adapted, woody, perennial plant species with current distributions that overlap in the coastal chaparral ecoregion of southern California. We focused on two long-lived, fire-resistant oak tree species, one with a narrow range in the southeast chaparral (*Quercus engelmannii*) and the other with a broad range spanning much of the California coast (*Q. agrifolia*); two long-lived coniferous pine tree species that are fairly resistant to fire when they are large, both with broad, partially overlapping ranges across Californian montane forests (*P. jeffreyi*, *P. lambertiana*); and two obligate-seeding shrub species in the southeast chaparral, one with a very narrow range (*Ceanothus verrucosus*) and the other with a relatively broader range (*C. perplexans*). For each of these species, we identified accessible published data for building demographic population models (van Mantgem and Stephenson 2005; Lawson et al. 2010; Legras et al. 2010; Regan et al. 2010; Maloney et al. 2011; Conlisk et al. 2012; Syphard et al. 2013; Davis et al. 2019).

2.3 | Distribution Models—Current and Future Habitat

We created maps of species' habitats over space and time at 270-m spatial resolution by generating SDMs for each species. Detailed descriptions of these SDMs can be found in Rose et al. (2023). To build the SDMs, we used presence-absence data from vegetation surveys (provided by California Fish and Wildlife and Dr. James Thorne, pers. comm.), all collected between 1980 and 2019. As predictor variables in our SDMs, we selected a set of climatic, hydrologic, terrain, and soil variables associated with plant distributions in water-limited ecosystems such as California (Stephenson 1998; Dubuis et al. 2013; Kueppers et al. 2005). This included climatic water deficit, actual evapotranspiration, minimum monthly temperature, wet- and dry-season precipitation, soil pH, available water-holding capacity, soil depth, percent clay, and landform type (see Rose et al. 2023). Hydroclimatic variables reflected 30-year averages for the time period 1980–2010 and were produced by the Basin Characterisation Model (Flint et al. 2021). Using the habitat suitability maps generated for 1980–2010, we delineated occupied suitable habitat maps to be used as the baseline habitat for each species.

To project maps of future suitable habitat, we used climate projections from each combination of two representative concentration pathway emissions scenarios (RCP) under two different global circulation models (GCM). We chose these projections to represent a range of emissions outcomes (RCP 4.5—moderate; RCP 8.5—high) and a range of climatic conditions in California (CNRM-CM5—warm/wet; HadGEM2-ES—hot/dry; Pierce et al. 2018). We projected the SDMs to the years 2055 (midcentury, averaged between 2040 and 2069) and 2085 (end-of-century, averaged between 2070 and 2099) and interpolated habitat suitability for intervening years (between 1995 and 2055 and between 2055 and 2085). To evaluate habitat suitability and demographic processes in locations where the species are currently found, we restricted all future suitability maps to the extent of the initial distribution. Though no-dispersal models of only in situ habitat changes underestimate future population sizes (Urban et al. 2013; Urban 2024), we made this assumption because the longer generation time and short dispersal distances of plants in this study suggest that they would be unlikely to track climate change on their own (Corlett and Westcott 2013). All SDMs were constructed in R version 4.2.0 using the *flexsdm* package (R Core Team 2022; Velazco et al. 2022).

As in Rose et al. (2023), we incorporated land use and land-use change into our distribution models by using the HadGEM2-ES RCP 4.5 and 8.5 scenarios from the Integrated Climate Land Use Scenario (ICLUS) (Theobald 2005; Bierwagen et al. 2010).

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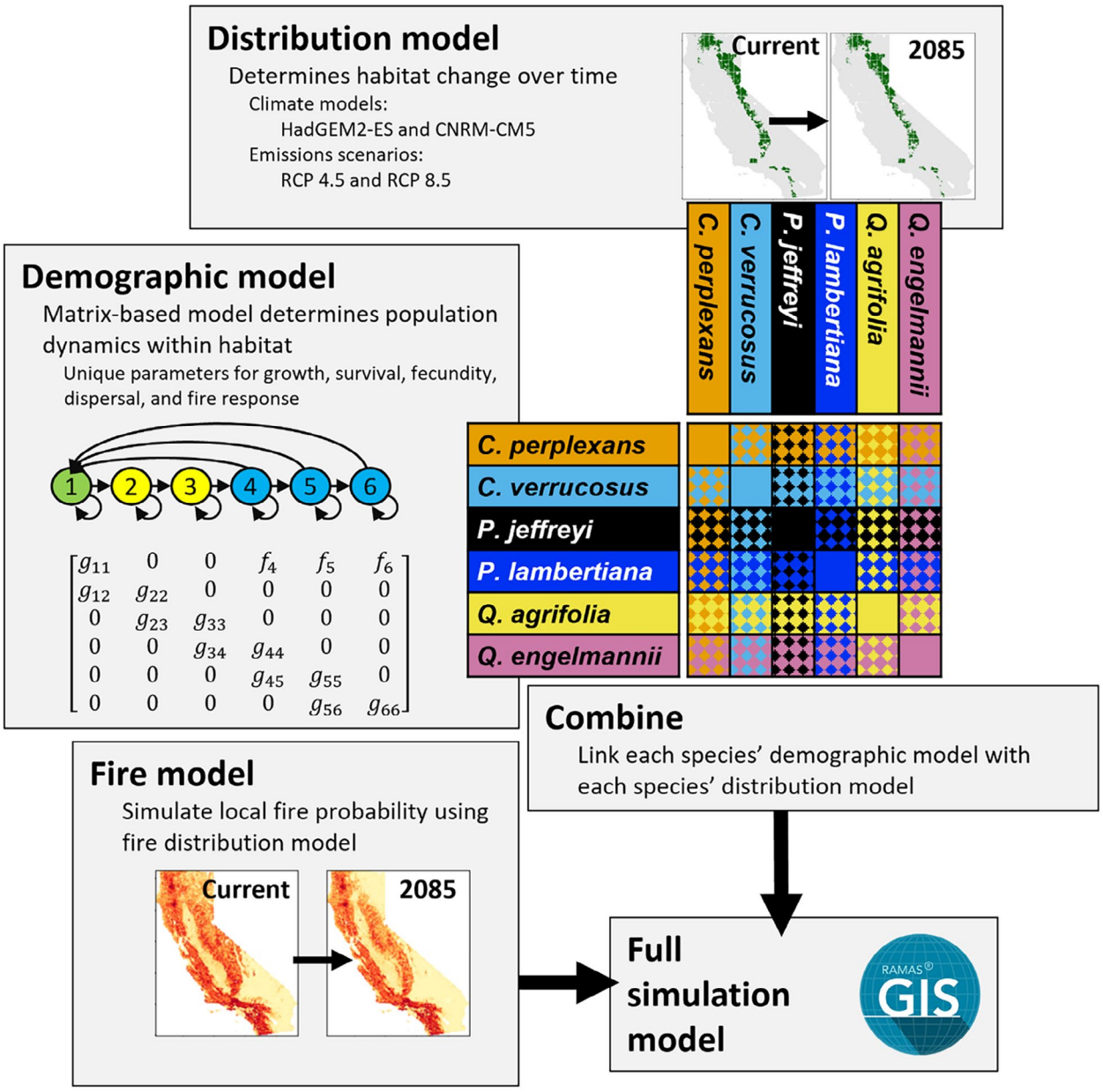


FIGURE 1 | Summary of modelling methodology: demographic models were stochastic, stage-structured population models with unique parameters for each species. Species distribution models were based on species' presence/absence under baseline climate and projected into future bioclimatic variables. The fire model simulated local fire occurrences based on a fire distribution model that estimates future fire probabilities from bioclimatic variables and other geographic variables. Each demographic model simulated unique species' responses to fire occurrences. By combining each demographic model with each simulation model and simulating population dynamics, we were able to investigate which populations changed as a result of ecological characteristics versus geographic trends.

Simplifying each land-use category's impact on habitat suitability produced by the SDMs, we estimated that cells with natural land use would have no impact on habitat suitability; cells within the exurban category would reduce habitat suitability by 50%; and cells classified as developed or crop agriculture would be unsuitable (suitability value of 0).

We used these SDMs to circumscribe the spatial and temporal structure of the population dynamics for each species. We used the habitat suitability values to scale the estimated carrying capacity of each 270 m × 270 m grid cell from 1995 to 2085. Evidence for whether habitat suitability from SDMs is correlated with population abundance or carrying capacity is mixed (Canham and Thomas 2010; Thuiller et al. 2014; Zurell et al. 2016; Weber et al. 2017; Dallas and Hastings 2018; Lee-Yaw et al. 2022). However, the strength of this relationship may depend on the spatial scale of the models (Brambilla et al. 2024). Moreover, SDMs may effectively represent the upper limit of population abundance in some situations (VanDerWal et al. 2009; Monnier-Corbel et al. 2023). This approach of linking carrying capacity to habitat suitability may overestimate population abundances, especially within the centre of the species' range (Dallas et al. 2017). While we focus our analysis on the differences between demographic models rather than estimating

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realistic population changes, this assumption may still overestimate abundances when habitat suitability is high and underestimate abundances when habitat suitability is low.

Though realistic population structure would vary between species, we constructed each species to have a similar overall structure to facilitate comparisons between models. We grouped cells into larger patches, defined as distinct clusters of cells that were within a two-cell radius of each other, which served as distinct subpopulations in our model. However, using these criteria, the overall population structure for each species generally consisted of several smaller subpopulations and some very large subpopulations. Because large numbers of very small patches did not contribute to overall abundance in a meaningful way, we excluded patches where the total habitat suitability of all cells in the patch was <5. Conversely, large subpopulations encompassed high spatial heterogeneity hundreds of kilometres across; making it necessary to further separate large patches. Therefore, we placed a lattice across California that partitioned the overall species' range into smaller subpopulation patches. This lattice artificially created a series of vertical and horizontal lines of unsuitable habitat, 2 cells wide with 30 cells of potentially suitable habitat in between.

The total carrying capacity and shape of these patches changed as suitable habitat changed over time. Some patches fragmented into multiple patches as the habitat suitability of individual cells declined. When patches fragmented into separate subpopulations, the current subpopulation abundance and stage structure were distributed relative to the newly created patches' carrying capacities. We then applied distinct population dynamics in the newly created subpopulations. To keep consistent comparisons for analysis, we later pooled together all subpatches that originated from the same patch.

2.4 | Wildfire Model

We modelled wildfire occurrences in each subpopulation as random independent events. During each two-year time step, t, a stochastic process generated wildfire occurrences for each subpopulation patch, x, with probability $p_2(x,t)$. To determine $p_2(x,t)$, we used results from a fire distribution model (FDM) across California (Syphard et al. 2024). This model, trained from fire occurrences across California from 1981 to 2010, predicts the probability of fire occurrence using the Maxent algorithm based on a suite of climate, terrain, and land-use predictor variables. We used a version of the FDM that included ecoregion as a predictor variable to avoid bias from arid desert ecoregions with low fire probability. Under each climate model (CNRM-CM5/HadGEM2-ES) and emissions scenario (RCP 4.5/RCP 8.5), this FDM gave us 30-year fire occurrence probabilities $p_{30}(x,t)$ for three time periods: 1980–2010, 2040–2069 and 2070–2099. We converted these into per-time-step (2-year) fire probabilities $p_2(x,t)$ by assuming wildfire occurrence is a binomial variable:

$$p_2(x,t) = 1 - \left[1 - p_{30}(x,t)\right]^{1/15} \tag{1}$$

For each species' population structure, we used the initial patch perimeter and found the average value of $p_2(x,t)$ for each time period under each climate projection. In our demographic models, we used baseline time period FDM probabilities (1980–2010) for the model burn-in period to the beginning of the climate change simulation. We used the 2040–2069 and 2070–2099 FDM probabilities for the years 2055 and 2085, respectively, and linearly interpolated all years between each of these points.

2.5 | Demographic Models—Population Dynamics

Each demographic model was a stochastic simulation of stage-structured population dynamics with density dependence, adapted from published demographic models and demographic data (van Mantgem and Stephenson 2005; Lawson et al. 2010; Legras et al. 2010; Regan et al. 2010; Maloney et al. 2011; Syphard et al. 2013; Conlisk et al. 2012; Davis et al. 2019). We derived survival, transition, and fecundity rates from these previous studies and converted all stage-structured models to have 2-year time steps (Methods S1). Because we derived each of these models from a small number of local populations over only a few years, they cannot realistically represent range-wide population dynamics for an entire species. Therefore, it is important to note that we are using these models to make broad comparisons of differences across demographic models and not realistic population projections.

During each time step, we used a species-specific matrix model with baseline mean values for survival, transition, and fecundity parameters for each subpopulation. This baseline transition matrix is a deterministic version of the demographic population model in absence of fire and variability. In a generalised form, each model would have n stage classes, with the first stage class representing seeds or first-year seedlings. The mean probability of an individual in stage i transitioning into stage j within two years is g_{ij}. For any stage after the first, there can also be a mean fecundity rate, f_i. In general, the matrix models are in the form of the $n \times n$ matrix:

$$\begin{bmatrix} g_{1,1} & f_2 & \cdots & f_{n-1} & f_n \\ g_{1,2} & g_{2,2} & \cdots & g_{n-1,2} & g_{n,2} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ g_{1,n-1} & g_{2,n-1} & \cdots & g_{n-1,n-1} & g_{n,n-1} \\ g_{1,n} & g_{2,n} & \cdots & g_{n-1,n} & g_{n,n} \end{bmatrix} \tag{2}$$

There was additional environmental stochasticity around mean transition probabilities and fecundity values. We used a $n \times n$ standard deviation matrix, where s_{ij} is the standard deviation in transition probability from stage i to stage j, and q_i is the standard deviation in fecundity. Altogether for each time step, the transition from stage i to stage j before density dependence was a normal random variable with a mean g_{ij} and standard deviation s_{ij} (but set to 0 if <0 or 1 if >1). Similarly, the fecundity of stage i was a normal random variable with mean f_i and standard deviation q_j (but set to 0 if <0). After these values were randomly selected in each time step in each replication, we also incorporated demographic stochasticity via a binomial process for survival/transition and a Poisson process for fecundity. In these models, population density is limited by space, so we weighted the overall population density such that larger stage classes contributed more to carrying capacity than smaller stage classes. Whenever weighted population densities exceeded the carrying capacity,

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we applied a penalty on survival and transition probabilities so the subpopulation would gradually decline to carrying capacity. We weighted this penalty more severely on smaller stage classes to reflect competition for light (Conlisk et al. 2012).

During time steps in which fires occurred in a patch, we modified the mean transition matrix of the subpopulation. For the obligate seeding ceanothus species, 99% of all stems in subpopulations would be killed by the wildfire. A proportion of seeds in the seedbank would germinate during the same time step, as they would not normally germinate in absence of fire (Regan et al. 2010; Syphard et al. 2013). For pines, a proportion of trees in the subpopulation would be killed by wildfire, and larger trees were more resilient to this increased mortality. Moreover, in time steps following wildfire, larger pines suffered increased mortality from beetles (Fettig et al. 2010), and seedling establishment and survival of smaller size classes increased in response to increased exposure to sunlight (Kauffman 1986). Similarly, oaks would be resilient to fire, but would also experience some backward transitions to physiologically smaller size classes to simulate resprouting (Conlisk et al. 2012). Again, exposure to sunlight would increase the transition probabilities of smaller trees following a fire (Conlisk et al. 2012).

For oak species, the mean fecundity varied in each time step to simulate masting (Conlisk et al. 2012). The masting scenario for each oak was based on acorn counts from a field study by Davis et al. (2019) for *Q. agrifolia* and adapted from the California Acorn Survey Project for *Q. engelmannii* (Conlisk et al. 2012).

After producing offspring in the model, some seeds could disperse to nearby subpopulations. As noted previously, the SDMs we produced did not include long-distance dispersal that would lead to range expansion, as these species with long generation times and short dispersal kernels would be unlikely to keep pace with climate change (Corlett and Westcott 2013). Because even realistically minor range expansion would add substantial model complexity without much additional insight, we simplified demographic models to only include short-distance dispersal within species' baseline range. This assumption limits projections to changes within the baseline distribution. Pine and ceanothus species have very limited dispersal and were unlikely to disperse between patches on the spatial scale of our models (Holl et al. 2000; Johnson et al. 2003; Regan et al. 2010), so all seeds remained in the subpopulations in which they were produced. Birds may transport oaks further (Gomez 2003), and past models suggest that acorn dispersal between patches would have a small effect on population outcomes at the spatial resolution and scale of these models (Conlisk et al. 2012). Therefore, we allowed some dispersal between subpopulations where patch centroids were within 10 km of each other, but only with oak demographic models. The probability of dispersal decreased exponentially with higher distances between subpopulation patch centroids.

Using these demographic models, deterministic growth rates for oaks and pines were positive ($\lambda > 1$) without wildfire or density dependence. Thus, oak and pine populations generally declined during wildfire events before recovering toward carrying capacity, allowing sufficient time for the population to return to a reproductive age. Alternatively, populations of obligate-seeding ceanothus species would grow rapidly following wildfire events that cause germination while declining gradually via mortality until the next wildfire event.

2.6 | Implementation

For each of the six species, we linked each demographic model to each other species' distribution model. We ran 1000 replicate stochastic simulations of each combination of the two GCM climate models (CNRM-CM5, HadGEM2-ES) and two emissions scenarios (RCP 4.5, RCP 8.5). We used RAMAS GIS (Akçakaya and Root 2005) to convert distribution models into population patch structure and to simulate both fire occurrences and demographic models.

To create initial populations for each combination of demographic and distribution model, we simulated a 90 time-step (180-year) burn-in period in each subpopulation before simulating climate change. For oak and pine demographic models, we set subpopulations so their densities and carrying capacities were at a stable age distribution before the burn-in period. For ceanothus demographic models, we set each subpopulation to consist of post-germination 0–1 year seedlings before the burn-in period. For each replication, we used the resulting population size and structure in each patch at the end of the burn-in period as the initial population. We then ran the demographic population model for 45 time steps (90 years) over the climate change and fire projections. To reduce the high variability in population size caused by masting and fire-induced germination, the reported abundance of each subpopulation only included the number of saplings and adults for oak and pine species and only included reproductive adults for ceanothus species.

To compare the effect of dynamics in both the spatial distributions and demographic models on the relative change in total population and subpopulation abundance, we ran an ANOVA with the relative final abundance (final abundance divided by initial abundance) of extant populations as the dependent variable and the distribution model species and demographic model species as independent variables, where 'distribution model species' refers to the species on which the SDM is based and the 'demographic model species' refers to the species on which the demographic population model is based. Because relative final abundance can be sensitive to subpopulations with very small initial populations, we exclude all subpopulations with final relative abundances in the top 0.001 quantile from this analysis. Similarly, to compare the effect of habitat change on total population and subpopulation abundance, we ran a generalised linear model with the relative final abundance of extant populations as the dependent variable and the relative habitat change (final habitat suitability divided by initial habitat suitability) and demographic model species as independent variables, again, excluding the top 0.001 quantile of relative abundances.

Finally, for each combination of GCM, emissions scenario, and distribution model, we calculated the coefficient of variation of the relative final abundances across all demographic models for each subpopulation within a given distribution model. If there were large differences between demographic models and these differences contributed to subpopulation-level outcomes, then

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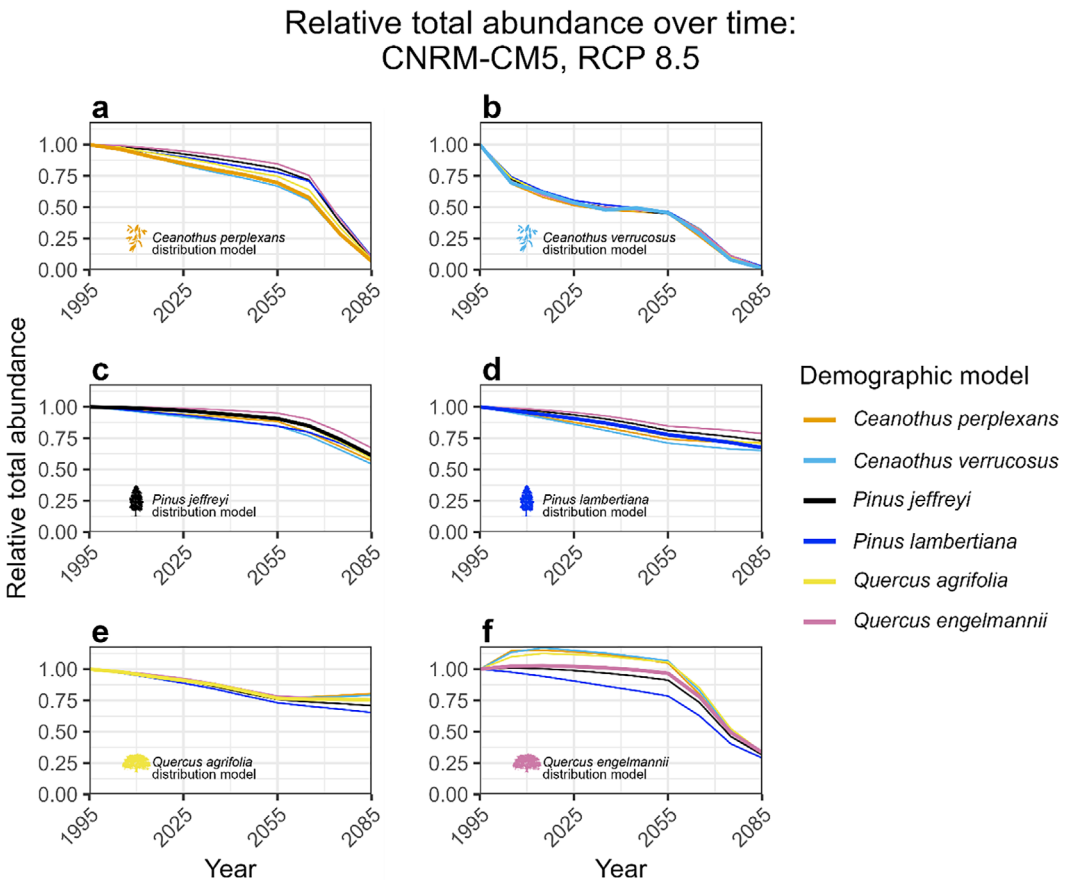


FIGURE 2 | Relative abundance over time of the total population of all demographic models linked each distribution model under the CNRM-CM5, RCP 8.5 climate projection, averaged across 1000 stochastic simulations. (a–f) Each panel represents a different distribution model. Each colour represents a different demographic model linked to the distribution model. The matching demographic model is bolded for emphasis.

this coefficient of variation could represent the importance of demography on that subpopulation. Because wildfire response varied between demographic models, we performed a linear regression with this coefficient of variation as the dependent variable and the initial probability of wildfire in the subpopulation as the independent variable. To meet assumptions of normality, we log-transformed the dependent variable and excluded subpopulations in the top 0.001 quantile of relative abundances.

3 | Results

We found that both total population and subpopulation abundances declined along with habitat suitability over the time horizon for all species, with these trajectories showing some dependency on both the demographic and distribution models (Figures 2 and 3). An ANOVA revealed that at the total population level, differences in species' geography (distribution model) had a significant effect on final abundances, while species' demography generally had no significant effect across each climate projection (Table 1). In contrast, at the subpopulation level, both models were highly significant, meaning that SDMs alone were insufficient to predict subpopulation level outcomes (Table 2). Moreover, a set of general linear models found that lower habitat suitability from the SDM consistently led to lower abundance at both the total population and subpopulation levels (Table 1; Figure 3, Figures S1–S4). In these linear models, the demographic model only consistently played a significant role in influencing the final relative abundances (Table 2; Figure 3, Figures S5–S10). The general results of this linear model were consistent across all climate projections and emissions scenarios.

Overall, we found that variation between the outputs of demographic models was largely associated with projected wildfire probability (Figure 4, Figures S11–S14). For each SDM and climate projection, it was revealed that areas with currently higher predicted wildfire probabilities generally exhibited greater variability in final subpopulation abundances across demographic models for all species except *C. verrucosus* (with small sample sizes ≤ 5 subpopulations; Table 3). This positive relationship between fire probability and coefficient of variation in the relative final abundance was consistent across the specific distribution model (besides *C. verrucosus*) and climate projection (Tables S1–S4).

We found underlying geographic patterns in the importance of demography across species, generally following the geographic patterns of wildfire dynamics (Figure 5, Figures S15–20). That is, areas with higher wildfire probability were generally the same areas with high variance in final relative subpopulation abundances. Moreover, differences in demographic models could determine whether subpopulations would consistently grow or decline within a particular region (Figure 6). In many cases, habitat suitability declined within a subpopulation, but some demographic models were associated with an increased relative abundance

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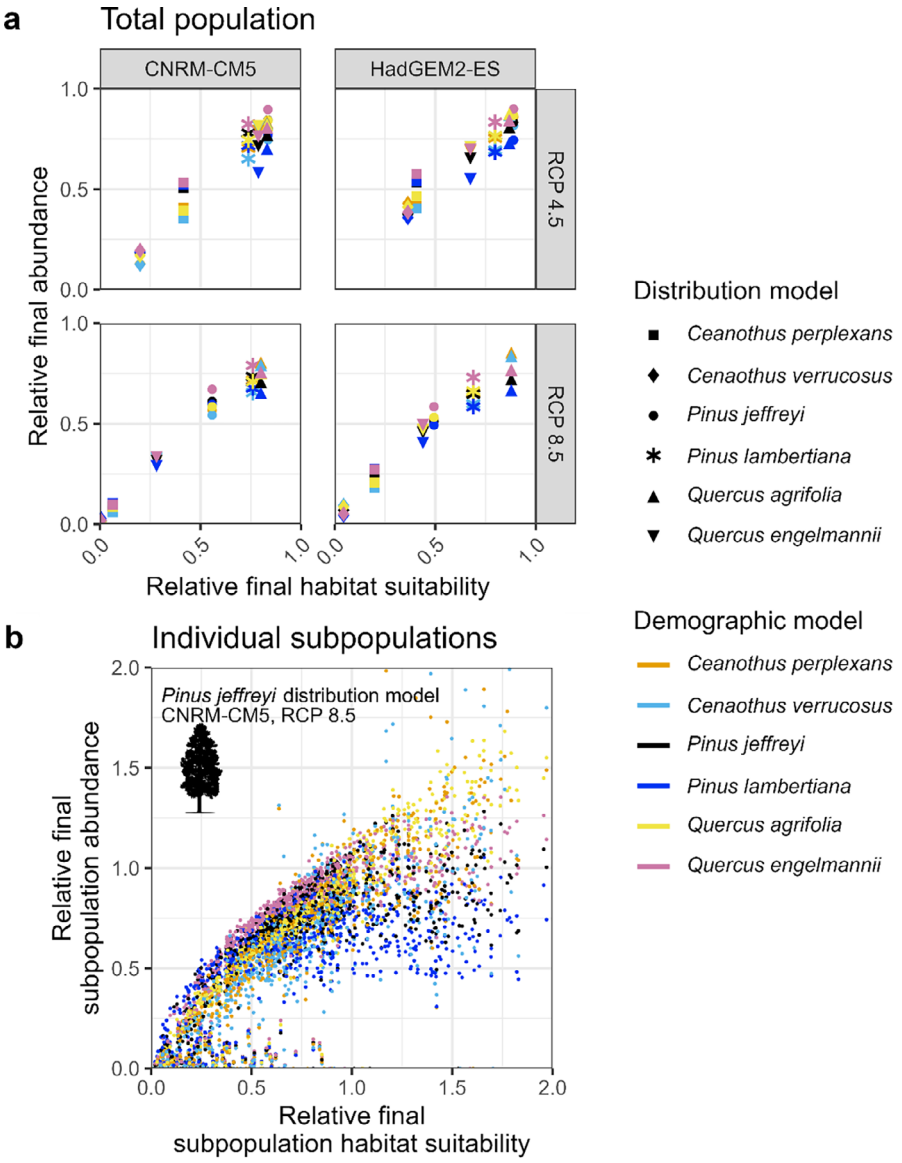


FIGURE 3 | Average relative final abundance across 1000 simulations compared to the relative final habitat suitability, across the entire species' range (a) or across subpopulations of the *Pinus jeffreyi* distribution model (b). Each colour represents a different demographic model and each shape represents a different distribution model. (a) Each panel represents a different combination of GCM climate model and RCP emissions scenario. Between the plots, all combinations of six distribution and demographic models are shown with four climate projections represented. (b) Individual subpopulation results from each demographic model linked to the *P. jeffreyi* distribution model under the CNRM-CM5 RCP 8.5 climate projection.

while others declined. Similarly, habitat suitability could increase within a subpopulation while demographic models simultaneously predicted both increasing and decreasing abundances.

4 | Discussion

We found that the range-wide population abundance of each of these six plant species in the CFP is likely to decline as their habitat suitabilities decline due to climate and land-use change in the coming century. This overall decline occurred under all climate projections in our models, irrespective of the life history characteristics of the species, suggesting that climate and land-use change would be the primary drivers of population decline across the scale of the entire species. However, life history differences between the species influenced changes in abundance at the scale of individual subpopulations, revealing the importance of species' demography at the subpopulation level but not the total population level. That is, even when habitat suitability decline was identical in a hypothetical subpopulation, species-specific population dynamics caused wide variance in final abundance outcomes. These differences in demography were largely driven by each species' response to fire and the distribution of wildfire dynamics within their range.

4.1 | Demography Versus Geography

Our results emphasise that there are subpopulation-level geographic patterns in our integrated models, highlighting the importance of species' demography under climate change, and these patterns are separate from a species' environmental

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TABLE 1 | Linear model results for the effect of explanatory variables on the mean relative final total population abundance for each combination of global circulation model (GCM) and emissions scenario (RCP). distModelSp and demModelsp are categorical variables determining the species of the distribution model and the demographic model, respectively. relK is the relative final carrying capacity of the total population.

Climate model	Emissions scenario	*n*	R^2	Term	df	*F* stat.	*p*
Statistical model: relN~distModelSp+demModelSp							
CNRM-CM5	RCP 4.5	36	0.959		10, 25	59.1	< 0.0000001
				distModelSp	5	116	< 0.0000001
				demModelSp	5	1.96	0.120
CNRM-CM5	RCP 8.5	36	0.990		10, 25	260	< 0.0000001
				distModelSp	5	518	< 0.0000001
				demModelSp	5	1.77	0.156
HadGEM2-ES	RCP 4.5	36	0.953		10, 25	51.1	< 0.0000001
				distModelSp	5	98.4	< 0.0000001
				demModelSp	5	3.74	0.015
HadGEM2-ES	RCP 8.5	36	0.981		10, 25	129	< 0.0000001
				distModelSp	5	256	< 0.0000001
				demModelSp	5	2.24	0.0816
Statistical model: relN~relK+demModelSp							
CNRM-CM5	RCP 4.5	36	0.947		6, 29	87	< 0.0000001
				relK	1	513	< 0.0000001
				demModelSp	5	1.75	0.154
CNRM-CM5	RCP 8.5	36	0.981		6, 29	252	< 0.0000001
				relK	1	1507	< 0.0000001
				demModelSp	5	1.04	0.414
HadGEM2-ES	RCP 4.5	36	0.938		6, 29	72.8	< 0.0000001
				relK	1	420	< 0.0000001
				demModelSp	5	3.25	0.0188
HadGEM2-ES	RCP 8.5	36	0.967		6, 29	141	< 0.0000001
				relK	1	838	< 0.0000001
				demModelSp	5	1.49	0.224

niche. For example, when we consider a group of subpopulations on the northern end of the range for *P. jeffreyi*, habitat suitability is largely expected to increase (Figure 6). This might suggest this location is a leading edge of range expansion or refugia under climate change. If we assume the species' population dynamics would follow the demography of oak species or ceanothus species (as simplified by our models), this increase in habitat suitability would correspond to an increase in abundance. However, when we used the demographic models for either pine species, the subpopulations mostly remained stable or declined. Interestingly, the areas that might be considered a leading edge, stable, or trailing edge depend largely on which species' demographic model drives the population dynamics. In northwestern California, a population with the demography of a long-lived, fire-tolerant *Q. agrifolia* model would be most successful, especially in areas with higher fire probabilities. In the central Sierra Nevada mountains, several areas with low fire probability would benefit populations with a demography similar to the obligate seeding ceanothus shrubs over the demography of other species. In the southern Sierra Nevada, habitat suitability declined enough that this area would be considered a trailing edge for all demographic models, though a population with *Q. engelmannii* demography would consistently decline by the least amount. Of course, these hypothetical examples do not represent the life history of *P. jeffreyi*, but they do emphasise that different life history patterns could largely affect which areas of a species' range are likely to be threatened by climate change. By comparing different demographic models within the same distribution model, our results suggest that even when two species might have the same environmental niche, differences in demography alone can drive geographic patterns in range shift.

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TABLE 2 | Linear model results for the effect of explanatory variables on the relative final subpopulation abundance for each simulation in each combination of global circulation model (GCM) and emissions scenario (RCP). distModelSp and demModelsp are categorical variables determining the species of the distribution model and the demographic model, respectively. relK is the relative final carrying capacity of the subpopulation.

Climate model	Emissions scenario	*n*	R^2	Term	df	*F* stat.	*p*
Statistical model: relN~distModelSp+demModelSp							
CNRM-CM5	RCP 4.5	21,648	0.0732		10, 21,637	171	< 0.0000001
				distModelSp	5	219	< 0.0000001
				demModelSp	5	122	< 0.0000001
CNRM-CM5	RCP 8.5	19,350	0.0663		10, 19,339	137	< 0.0000001
				distModelSp	5	206	< 0.0000001
				demModelSp	5	69.2	< 0.0000001
HadGEM2-ES	RCP 4.5	21,282	0.0894		10, 21,271	209	< 0.0000001
				distModelSp	5	236	< 0.0000001
				demModelSp	5	182	< 0.0000001
HadGEM2-ES	RCP 8.5	17,718	0.0587		10, 17,707	110	< 0.0000001
				distModelSp	5	149	< 0.0000001
				demModelSp	5	72.0	< 0.0000001
Statistical model: relN~relK+demModelSp							
CNRM-CM5	RCP 4.5	21,648	0.524		6, 21,641	3990	< 0.0000001
				relK	1	22,734	< 0.0000001
				demModelSp	5	237	< 0.0000001
CNRM-CM5	RCP 8.5	19,350	0.555		6, 19,343	4013	< 0.0000001
				relK	1	23,559	< 0.0000001
				demModelSp	5	145	< 0.0000001
HadGEM2-ES	RCP 4.5	21,275	0.551		6, 21,275	4352	< 0.0000001
				relK	1	24,820	< 0.0000001
				demModelSp	5	365	< 0.0000001
HadGEM2-ES	RCP 8.5	17,718	0.493		6, 17,711	2872	< 0.0000001
				relK	1	16,781	< 0.0000001
				demModelSp	5	134	< 0.0000001

SDMs are generally effective at estimating where we expect to find a species based on environmental similarity to known occurrences, and they have been widely used to predict species' future distributions (Pearson and Dawson 2003; Dawson et al. 2011; Warren et al. 2018). However, SDMs are insufficient to predict population abundance and demographic rates within those distributions (Csergő et al. 2017; Dallas and Hastings 2018; Le Squin et al. 2021; Lee-Yaw et al. 2022; Perret et al. 2024). Though there can be some relationship between species' occurrence and abundance, this relationship is inconsistent (Thuiller et al. 2010; Thuiller et al. 2014; Acevedo et al. 2017; Jiménez-Valverde et al. 2021). While we did not use SDMs to project population abundances directly in this study, using them to estimate carrying capacity directly influences the model used to estimate population abundances in the long term. Our models showed that demography was generally unimportant in predicting species vulnerability to global change scenarios at the range-wide, total population level, but demographic differences between species became more important at the scale of individual subpopulations. That is, over the timescale of our model, variation in demography and fire responses of the species we analysed did not substantially affect abundance overall but did at finer spatial scales. Because of limited demographic data, we could not explicitly incorporate localised demographic parameters, but further differentiation in locally adaptive dynamics and demography between subpopulations could reveal starker variability in projections (Hällfors et al. 2016; DeMarche et al. 2019). Because differences in demographic models in our study led to widely different results at the subpopulation level without having a significant effect on the total species abundance, these localised differences are critical as they could lead to substantial spatial variation in population projections for more realistic

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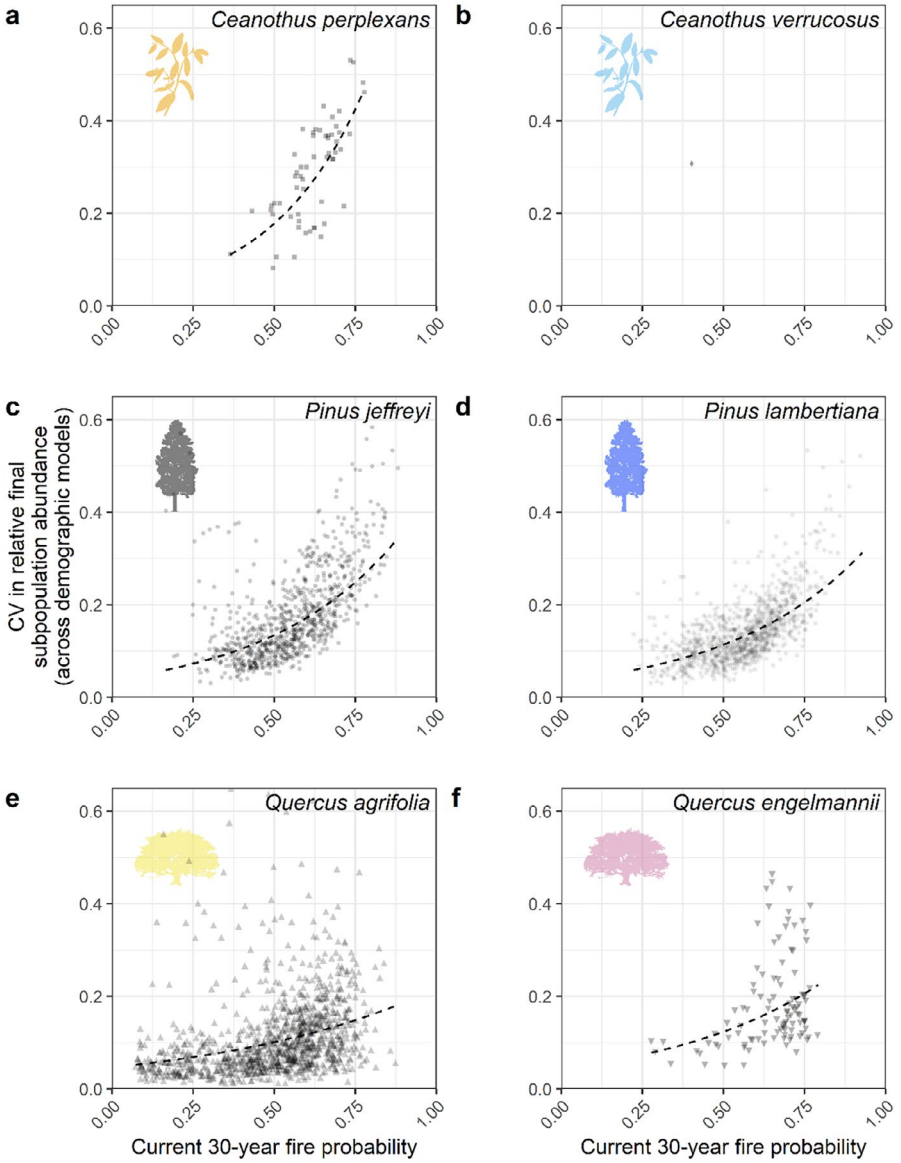


FIGURE 4 | Coefficient of variation of the final relative subpopulation abundance across all demographic models under single distribution models as they relate to estimated current wildfire probability under each demographic model and the CNRM-CM5 RCP 8.5 climate projection. (a–f) Each panel represents a different species' demographic model. Each point represents an individual subpopulation and lines represent the marginal effect of the variable under the linear model.

applications. Many recent studies focus on the importance of using SDMs in concert with population models before making conservation decisions (Briscoe et al. 2019; Franklin et al. 2021; Lee-Yaw et al. 2022). However, unlike our simplified approach of linking SDMs to carrying capacity and using a single demographic model over an entire species' range, an approach that adapts models to account for more localised differences in demographic processes across the species' range would be necessary in practice.

Our results suggest that even in a hypothetical case where the effect of climate change on habitat suitability is identical across species, demographic characteristics alone can dramatically change a population's response. Each species' growth, generation time, germination, dispersal capabilities, and density dependence could affect how population dynamics respond as habitat increases, decreases or fluctuates over time. For example, populations of obligate seeding species tend to grow in even-aged cohorts because of their dependence on fire for germination and the tendency for fire to kill standing plants (Keeley 1992; Zammit and Zedler 1993). Because of this, competition and density dependence tend to be most important soon after a fire event when germinants compete with many conspecifics (Pausas and Keeley 2014), especially compared with other species, like the pine species we modelled, that germinate and compete in intervening years. With heavy competition for space and limited opportunities to replenish any lost population due to the reliance on fire for germination, obligate seeding populations might decline more quickly with habitat loss and increase more slowly into expanding habitat, if at all, given limited dispersal ability.

Oaks that are slow to reach maturity may change in population structure as habitat changes. Declining habitat quality

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TABLE 3 | Linear model results for the effect of current fire probability and relative change in fire probability on the logarithm of the coefficient of variation in relative final abundance for each subpopulation across all demographic models with the CNRM-CM5 RCP 8.5 climate projection. initFireProb is the initial probability of wildfire over 30 years in each subpopulation.

Distribution model	*n*	R^2	df	*F* stat.	Term	SE	Estimate	*t* stat.	*p*
Ceanothus perplexans	58	0.472	56	50.0					< 0.0000001
					Intercept	0.307	−3.47	−11.3	< 0.0000001
					initFireProb	0.492	3.48	7.07	< 0.0000001
Ceanothus verrucosus	1	—	—	—					—
					Intercept	—	—	—	—
					initFireProb	—	—	—	—
Pinus jeffreyi	830	0.382	828	513					< 0.0000001
					Intercept	0.0613	−3.24	−52.8	< 0.0000001
					initFireProb	0.109	2.46	22.6	< 0.0000001
Pinus lambertiana	1085	0.416	1083	773					< 0.0000001
					Intercept	0.0486	−3.35	−69.0	< 0.0000001
					initFireProb	0.0849	2.36	27.8	< 0.0000001
Quercus agrifolia	1144	0.0977	1142	124					< 0.0000001
					Intercept	0.0729	−3.07	−42.1	< 0.0000001
					initFireProb	0.139	1.54	11.1	< 0.0000001
Quercus engelmannii	107	0.155	105	19.2					< 0.0000001
					Intercept	0.306	−3.12	−10.2	< 0.0000001
					initFireProb	0.468	2.05	4.39	0.0000274

could mean that only larger, mature adults persist while fewer seedlings and saplings establish and persist, exacerbating what is sometimes referred to as a 'regeneration problem' (Sudworth 1908). Though there is mixed evidence that this regeneration problem currently affects California plant species (Tyler et al. 2006), climate change combined with the 'interval squeeze' of less time to regenerate between wildfire occurrences could result in a substantial change in demographic age structure of these species across their ranges (Enright et al. 2015). Beyond this, each species' unique responses to the shifting climate and fire regimes should be especially important in areas where these shifts are more extreme.

4.2 | Wildfire

Our results, with wildfire dynamics based on a fire distribution model (Syphard et al. 2024), reflect the multifaceted interplay between wildfire patterns, climatic factors, and plant community distributions. Shifting fire regimes can be exacerbated by widely varying distributions of plant communities (Keeley and Syphard 2015, 2016, 2017, 2019) and human activity across California (Syphard et al. 2007, 2009; Parisien et al. 2016; Balch et al. 2017), and heterogeneously shifting fire regimes could influence the fate of plant species. In particular, the variability in subpopulation abundances across different demographic models underscores that unique demographic characteristics of a species are accentuated in areas where wildfires are more likely. Illustrating this with our results for the distribution model for *Pinus jeffreyi* and the CNRM-CM5 RCP 8.5 climate projection (Figure 5), there is higher variation among demographic models centred around areas in the Sierra Nevada and Cascades with historically higher fire probabilities. Within these high-variation subpopulations, our model generally predicted subpopulation abundance to decline yet remain extant under relatively high wildfire probabilities. *Pinus jeffreyi* has adaptations to resist frequent, low-intensity, fire-induced mortality, including thick bark that trees can shed when they are burning (Lanner 1983), but fire occurrences will have little direct benefit for the species.

Another species we modelled within the same distribution, *C. perplexans*, is an obligate seeding shrub that requires fire to germinate (Zammit and Zedler 1993). Obligate seeding species are generally better adapted to areas of more infrequent fire that allow sufficient time for seed bank establishment between fires. Frequent wildfire can kill an even-aged stand of ceanothus before it reaches maturity and produces seeds, causing local extinction (Jacobsen et al. 2004). Because of this, optimal fire frequencies for obligate seeding species are those that enable them to survive to maturity while also providing germination opportunities (Regan et al. 2010; Franklin et al. 2014). Obligate seeding species are particularly vulnerable to population decline and local extinction from fire regimes that shift with climate change (Bowman et al. 2016). Considering that wildfire could become more frequent in mountainous northern California in the coming century, albeit with high uncertainty in predictions

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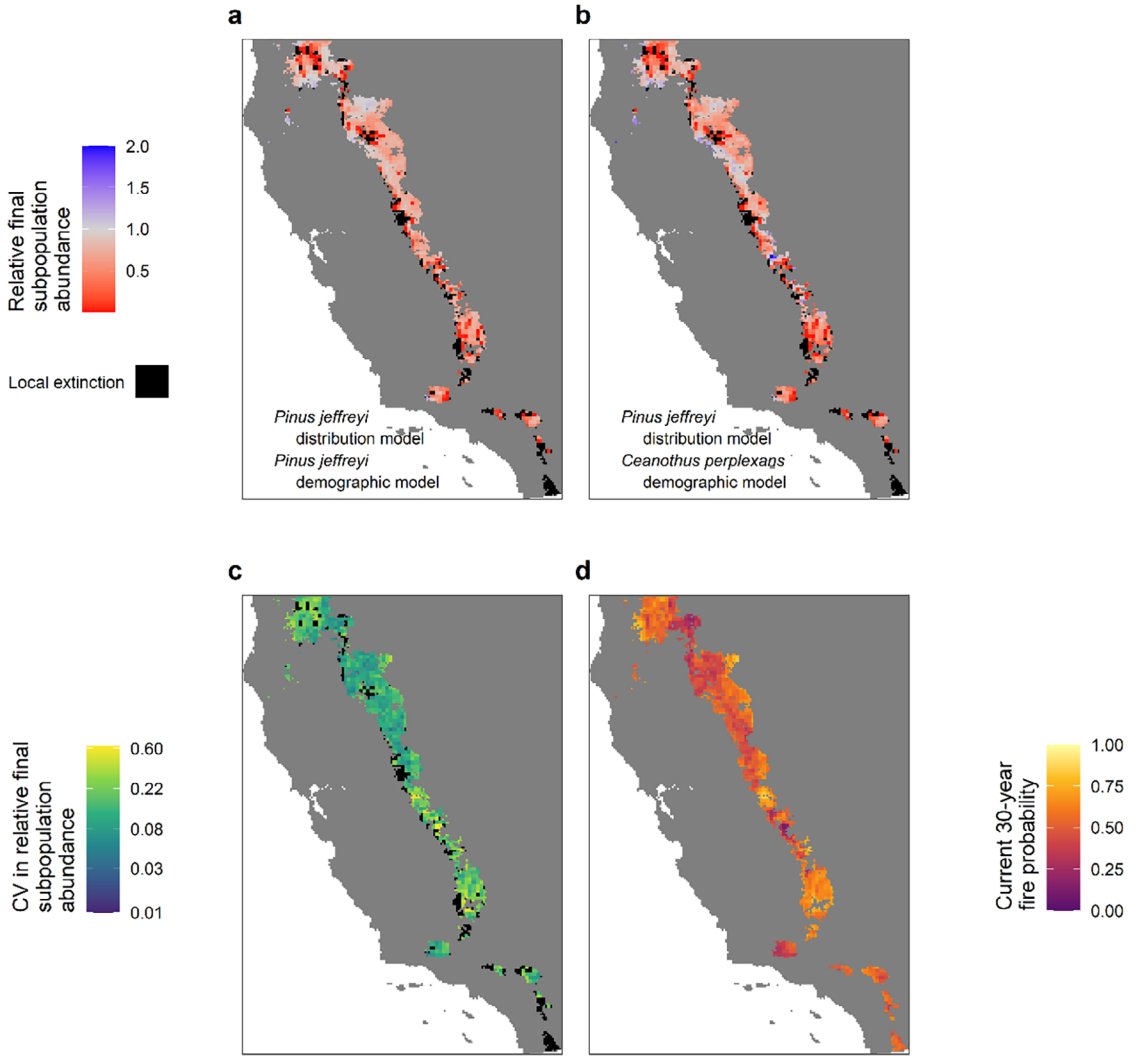


FIGURE 5 | Geographic distribution of subpopulation-level results for *Pinus jeffreyi* distribution model under CNRM-CM5 RCP 8.5 climate projection compared with geographic distribution of fire probabilities. Maps in (a) and (b) show the relative final abundance of subpopulation-level outcomes when using the *P. jeffreyi* demographic model (a) and the *Ceanothus perplexans* demographic model (b). Map (c) shows the coefficient of variation in relative final abundance across all demographic models. Map (d) shows current projected fire probabilities over a 30-year period within the species' current distribution.

(Fried et al. 2004; Westerling and Bryant 2008), shifting wildfire dynamics could create unsuitable conditions for many species that may be suitable to others.

4.3 | Conservation

Overall, our results reflect the complexity of plant species' responses to climate change, suggesting that species-specific life history characteristics matter (Parmesan and Hanley 2015) in addition to the geography of their exposure. Understanding the degree of population decline, its variance across models, and how these are geographically distributed might inform conservation actions. For example, some simulated subpopulations were unlikely to persist under global change irrespective of their demographic characteristics. In these subpopulations, species' survival, fecundity, or fire response would be unlikely to counteract changes in climate or land use that cause habitat to be unsuitable. Instead of conserving these subpopulations in situ, it might be preferable to relocate them to other places that are consistently predicted to have a high probability of persisting (Regan et al. 2012; Bonebrake et al. 2014; Backus et al. 2022).

In areas where subpopulations might decline, but with high variation between demographic models, in situ approaches might be worth investigating. Further analysis of parameter sensitivity could highlight which aspects of species' demography are driving the variation across demographic models. If variation is due to model sensitivity in recruitment, supplementing with seedlings from other subpopulations, preventing seed and seedling predation, or removing pest species could mitigate population decline. If variation is caused by model sensitivity to fire response, managing the impact of wildfire in these areas might prevent local extinction. Considering that most fire management strategies for California focus on forested areas and a majority of California's wildlands are not forested, additional research into fire management should be a priority (Keeley 2002; Schwartz and Syphard 2021).

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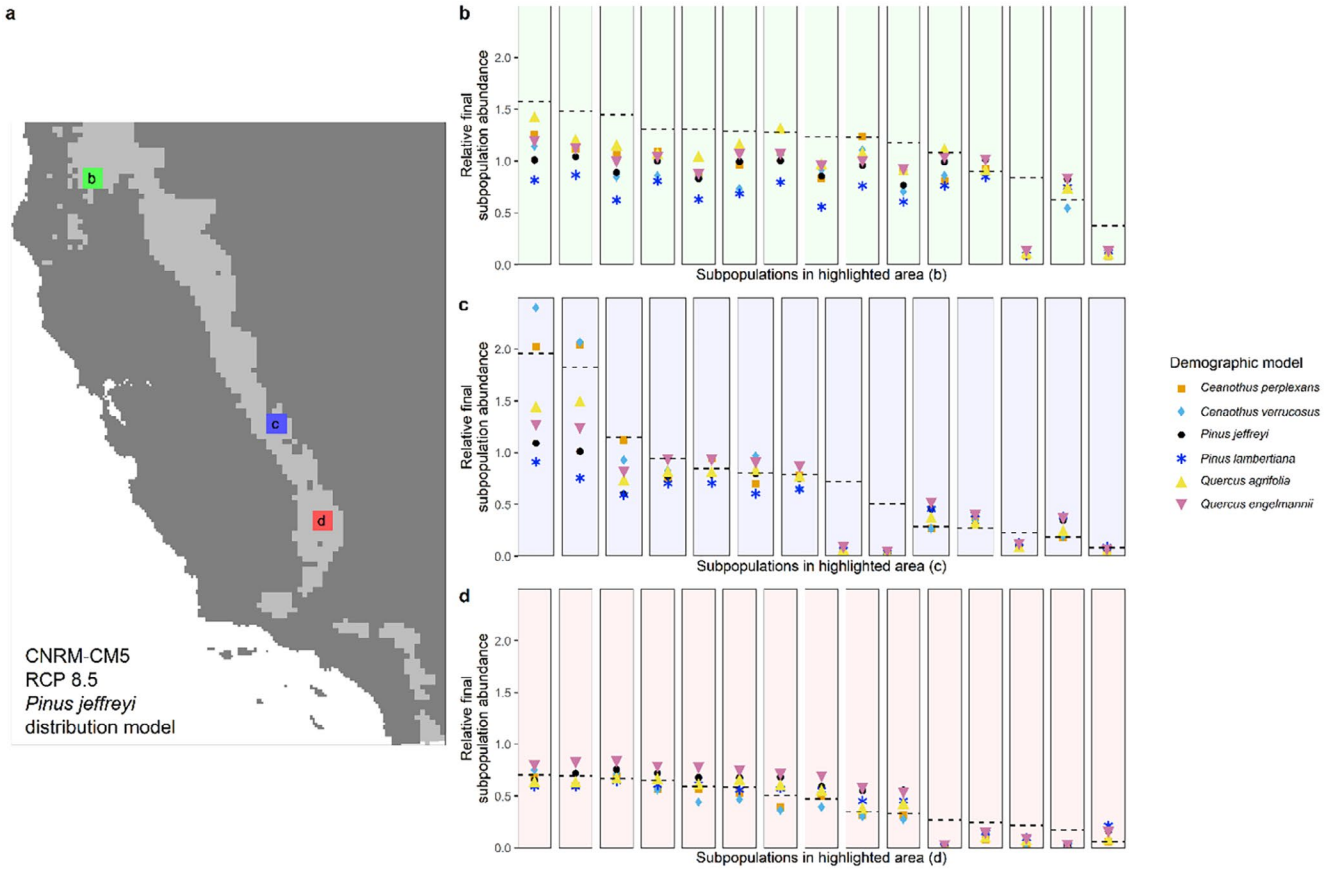


FIGURE 6 | Differences in final relative abundances within subpopulations estimated with each species' demographic model, using the *Pinus jeffreyi* spatial distribution model under the CNRM-CM5 RCP 8.5 climate projection. (a) Outline of the current binarised projected species distribution of *P. jeffreyi* with three groups of subpopulations highlighted. These groups correspond to results in following panels. (b–d) Final relative abundances of each non-extirpated subpopulation within the highlighted regions. Different shapes/colours correspond to results generated with different demographic models within the same distribution model. Dashed horizontal lines represent relative change in habitat suitability, as determined by the *P. jeffreyi* species distribution model.

Most plant species lack the life history data to generate even simplified demographic models like the ones we analysed in this study, so risk assessments are often based on habitat distribution models alone (Villero et al. 2017; Sofaer et al. 2019), which have limitations for conservation (Briscoe et al. 2019; Lee-Yaw et al. 2022). Demographic models require many years of measuring species' fecundity, germination, survival, growth, fire response, and dispersal throughout the longevity of a cohort. Ideally, measuring a wider range of individual subpopulations over more years and across the distribution of a species will result in a more sophisticated model, but obtaining such data can be challenging. Our models assumed that all demographic transitions and vital rates were consistent across space and species, depending only on carrying capacity derived from SDMs. Realistically, each of these demographic processes would vary over space, time, and environmental conditions, and these are not necessarily proportional to habitat suitability (Pironon et al. 2018; Bohner and Diez 2020). Demographic processes are far more complex than our simplified modelling approach, as higher suitability does not necessarily correlate with higher demographic rates. In particular, a metanalysis showed plant populations in lower suitability habitat had higher rates of retrogression and higher variability in demographic rates (Csergő et al. 2017). Without this type of demographic variability, models are likely to underestimate demographic responses in lower suitability habitats at the edge of a species range, leading to further complicating conservation implications. Other approaches to remedy the difficulty of combining demographic information with geography are to construct models that estimate demographic parameters over space using environmental predictors (Briscoe et al. 2019) such as demographic distribution models (Merow et al. 2014) or dynamic range models (Pagel and Schurr 2011). Moreover, climate change is ongoing, and plant species are already shifting and declining in California (Serra-Diaz et al. 2016; Madsen-Hepp et al. 2023) and across the globe (Chen et al. 2011; Zhu et al. 2012). Making conservation decisions with limited information will be necessary to conserve biodiversity.

Overall, plant species' responses to climate change will depend not only on where they are located and which climates they are adapted to, but also on how the species' unique life history characteristics allow them to persist, disperse, and adapt. We found that plant persistence might generally depend on how species-specific demographic characteristics interact with the geographic distribution of the species, as geography determines which environmental and anthropogenic stressors species are exposed to. Because these interactions are heterogeneous across multiple time and spatial scales, conserving each species regarding their unique demographic and geographic profiles might

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require local coordination. Supplementing large-scale, spatially explicit population models with smaller-scale examination of subpopulation characteristics, we might better identify the locations and functional types that will benefit the most from conservation management.

Author Contributions

G.A.B. and H.M.R. designed the original research idea. G.A.B., M.B.R., and S.J.E.V. built the models. G.A.B. analyzed the models and led the writing. All authors contributed to developing the research details, interpreting the results, writing the manuscript, and editing the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available on Dryad at https://doi.org/10.5061/dryad.k0p2ngfh7.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70067.

References

Acevedo, P., J. Ferreres, M. A. Escudero, J. Jimenez, M. Boadella, and J. Marco. 2017. "Population Dynamics Affect the Capacity of Species Distribution Models to Predict Species Abundance on a Local Scale." *Diversity and Distributions* 23: 1008–1017.

Ackerly, D. D., S. R. Loarie, W. K. Cornwell, et al. 2010. "The Geography of Climate Change: Implications for Conservation Biogeography." *Diversity and Distributions* 16: 476–487.

Akçakaya, H. R., and W. Root. 2005. *Applied Biomathematics*. Setauket.

Backus, G. A., Y. Huang, and M. L. Baskett. 2022. "Comparing Management Strategies for Conserving Communities of Climate-Threatened Species With a Stochastic Metacommunity Model." *Philosophical Transactions of the Royal Society B* 377: 20210380.

Backus, G. A., M. B. Rose, S. J. E. Velazco, J. Franklin, A. D. Syphard, and H. M. Regan. 2023. "Modeling the Effects of Spatially Explicit Patterns of Climate and Fire on Future Populations of a Fire-Dependent Plant." *Frontiers in Ecology and Evolution* 11: 1149509.

Balch, J. K., B. A. Bradley, J. T. Abatzoglou, R. C. Nagy, E. J. Fusco, and A. L. Mahood. 2017. "Human-Started Wildfires Expand the Fire Niche Across the United States." *National Academy of Sciences of the United States of America* 114: 2946–2951.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. "Impacts of Climate Change on the Future of Biodiversity." *Ecology Letters* 15: 365–377.

Bierwagen, B. G., D. M. Theobald, C. R. Pyke, et al. 2010. "National Housing and Impervious Surface Scenarios for Integrated Climate Impact Assessments." *Proceedings of the National Academy of Sciences of the United States of America* 107: 20887–20892.

Bohner, T., and J. Diez. 2020. "Extensive Mismatches Between Species Distributions and Performance and Their Relationship to Functional Traits." *Ecology Letters* 23: 33–44.

Bonebrake, T. C., A. D. Syphard, J. Franklin, et al. 2014. "Fire Management, Managed Relocation, and Land Conservation Options for Long-Lived Obligate Seeding Plants Under Global Changes in Climate, Urbanization, and Fire Regime." *Conservation Biology* 28: 1057–1067.

Bowman, D. M., C. A. Kolden, J. T. Abatzoglou, F. H. Johnston, G. R. van der Werf, and M. Flannigan. 2020. "Vegetation Fires in the Anthropocene." *Nature Reviews Earth and Environment* 1: 500–515.

Bowman, D. M. J. S., G. J. Williamson, L. D. Prior, and B. Murphy. 2016. "The Relative Importance of Intrinsic and Extrinsic Factors in the Decline of Obligate Seeder Forests." *Global Ecology and Biogeography* 25: 1166–1172.

Brambilla, M., G. Bazi, and L. Ilahiane. 2024. "The Effectiveness of Species Distribution Models in Predicting Local Abundance Depends on Model Grain Size." *Ecology* 105: e4224.

Briscoe, N. J., J. Elith, R. Salguero-Gómez, et al. 2019. "Forecasting Species Range Dynamics With Process-Explicit Models: Matching Methods to Applications." *Ecology Letters* 22: 1940–1956.

Brook, B. W., N. S. Sodhi, and C. J. Bradshaw. 2008. "Synergies Among Extinction Drivers Under Global Change." *Trends in Ecology & Evolution* 23: 453–460.

Canham, C. D., and R. Q. Thomas. 2010. "Frequency, Not Relative Abundance, of Temperate Tree Species Varies Along Climate Gradients in Eastern North America." *Ecology* 91: 3433–3440.

Chen, I. C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. "Rapid Range Shifts of Species Associated With High Levels of Climate Warming." *Science* 333: 1024–1026.

Conlisk, E., D. Lawson, A. D. Syphard, et al. 2012. "The Roles of Dispersal, Fecundity, and Predation in the Population Persistence of an Oak (*Quercus engelmannii*) Under Global Change." *PLoS One* 7: e36391.

Coop, J. D., S. A. Parks, C. S. Stevens-Rumann, et al. 2020. "Wildfire-Driven Forest Conversion in Western North American Landscapes." *Bioscience* 70: 659–673.

Corlett, R. T., and D. A. Westcott. 2013. "Will Plant Movements Keep Up With Climate Change?" *Trends in Ecology & Evolution* 28: 482–488.

Cowling, R. M., P. W. Rundel, B. B. Lamont, M. K. Arrayo, and M. Arianoutsou. 1996. "Plant Diversity in Mediterranean-Climate Regions." *Trends in Ecology & Evolution* 11: 362–366.

Crone, E. E., E. S. Menges, M. M. Ellis, et al. 2011. "How Do Plant Ecologists Use Matrix Population Models?" *Ecology Letters* 14: 1–8.

Csergő, A. M., R. Salguero-Gómez, O. Broennimann, et al. 2017. "Less Favourable Climates Constrain Demographic Strategies in Plants." *Ecology Letters* 20: 969–980.

Dallas, T. A., R. R. Decker, and A. Hastings. 2017. "Species Are Not Most Abundant in the Centre of Their Geographic Range or Climatic Niche." *Ecology Letters* 20: 1526–1533.

Dallas, T. A., and A. Hastings. 2018. "Habitat Suitability Estimated by Niche Models Is Largely Unrelated to Species Abundance." *Global Ecology and Biogeography* 27: 1448–1456.

14724642, 2025, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70067, Wiley Online Library on [21/08/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Davis, F. W., C. M. Tyler, and B. E. Mahall. 2019. "Demography of Evergreen and Deciduous Oaks in a Mixed Oak Savanna: Insights From a Long-Term Experiment." *Ecosphere* 10: e02570.

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. "Beyond Predictions: Biodiversity Conservation in a Changing Climate." *Science* 332: 53–58.

DeMarche, M. L., D. F. Doak, and W. F. Morris. 2019. "Incorporating Local Adaptation Into Forecasts of Species' Distribution and Abundance Under Climate Change." *Global Change Biology* 25: 775–793.

Doblas-Miranda, E., J. Martínez-Vilalta, F. Lloret, et al. 2015. "Reassessing Global Change Research Priorities in Mediterranean Terrestrial Ecosystems: How Far Have We Come and Where Do We Go From Here?" *Global Ecology and Biogeography* 24: 25–43.

Dubuis, A., S. Giovanettina, L. Pellissier, J. Pottier, P. Vittoz, and A. Guisan. 2013. "Improving the Prediction of Plant Species Distribution and Community Composition by Adding Edaphic to Topo-Climatic Variables." *Journal of Vegetation Science* 24: 593–606.

Enright, N. J., J. B. Fontaine, D. M. J. S. Bowman, R. A. Bradstock, and R. J. Williams. 2015. "Interval Squeeze: Altered Fire Regimes and Demographic Responses Interact to Threaten Woody Species Persistence as Climate Changes." *Frontiers in Ecology and the Environment* 13: 265–272.

Fettig, C., R. Borys, and C. Dabney. 2010. "Effects of Fire and Fire Surrogate Treatments on Bark Beetle-Caused Tree Mortality in the Southern Cascades, California." *Forest Science* 56: 60–73.

Flint, L. E., A. L. Flint, and M. A. Stern. 2021. "The Basin Characterization Model— A Monthly Regional Water Balance Software Package (BCMv8) Data Release and Model Archive for Hydrologic California: U.S. Geological Survey Data Release." https://doi.org/10.5066/P9PT36UI.

Franklin, J., H. M. Regan, and A. D. Syphard. 2014. "Linking Spatially Explicit Species Distribution and Population Models to Plan for the Persistence of Plant Species Under Global Change." *Environmental Conservation* 41: 97–109.

Franklin, J., H. M. Regan, and A. D. Syphard. 2021. "A Framework Linking Biogeography and Species Traits to Plant Species Vulnerability Under Global Change in Mediterranean-Type Ecosystems." *Frontiers of Biogeography* 13, no. 4: e51254.

Franklin, J., J. M. Serra-Diaz, A. D. Syphard, and H. M. Regan. 2017. "Big Data for Forecasting the Impacts of Global Change on Plant Communities." *Global Ecology and Biogeography* 26: 6–17.

Fried, J. S., M. S. Torn, and E. Mills. 2004. "The Impact of Climate Change on Wildfire Severity: A Regional Forecast for Northern California." *Climatic Change* 64: 169–191.

Gomez, J. M. 2003. "Spatial Patterns in Long-Distance Dispersal of *Quercus Ilex* Acorns by Jays in a Heterogeneous Landscape." *Ecography* 26: 573–584.

Hällfors, M. H., J. Liao, J. Dzurisin, et al. 2016. "Addressing Potential Local Adaptation in Species Distribution Models: Implications for Conservation Under Climate Change." *Ecological Applications* 26: 1154–1169.

Harrison, S., M. J. Spasojevic, and D. Li. 2020. "Climate and Plant Community Diversity in Space and Time." *Proceedings of the National Academy of Sciences of the United States of America* 117: 4464–4470.

Holl, K. D., H. N. Steele, M. H. Fusari, and L. R. Fox. 2000. "Seed Bank of Maritime Chaparral and Abandoned Roads: Potential for Vegetation Recovery." *Journal of the Torrey Botanical Society* 127: 207–220.

Jacobsen, A. L., S. D. Davis, and S. L. Fabritius. 2004. "Fire Frequency Impacts Non-Sprouting Chaparral Shrubs in the Santa Monica Mountains of Southern California." In *Ecology, Conservation and Management of Mediterranean Climate Ecosystems*. Millpress.

Jiménez-Valverde, A., P. Aragón, and J. M. Lobo. 2021. "Deconstructing the Abundance–Suitability Relationship in Species Distribution Modelling." *Global Ecology and Biogeography* 30: 327–338.

Johnson, M., S. B. Vander Wall, and M. Borchert. 2003. "A Comparative Analysis of Seed and Cone Characteristics and Seed-Dispersal Strategies of Three Pines in the Subsection *Sabinianae*." *Plant Ecology* 168: 69–84.

Kauffman, J. B. 1986. "The Ecological Response of the Shrub Component to Prescribed Burning in Mixed Conifer Ecosystems." Dissertation, University of California, Berkeley, CA.

Keeley, J. E. 1992. "Recruitment of Seedlings and Vegetative Sprouts in Unburned Chaparral." *Ecology* 73: 1194–1208.

Keeley, J. E. 2002. "Fire Management of California Shrubland Landscapes." *Environmental Management* 29: 395–408.

Keeley, J. E., J. G. Pausas, P. W. Rundel, W. J. Bond, and R. A. Bradstock. 2011. "Fire as an Evolutionary Pressure Shaping Plant Traits." *Trends in Plant Science* 16: 406–411.

Keeley, J. E., and A. D. Syphard. 2015. "Different Fire-Climate Relationships on Forested and Non-Forested Landscapes in the Sierra Nevada Ecoregion." *International Journal of Wildland Fire* 24: 27–36.

Keeley, J. E., and A. D. Syphard. 2016. "Climate Change and Future Fire Regimes: Examples From California." *Geosciences* 6: 37.

Keeley, J. E., and A. D. Syphard. 2017. "Different Historical Fire–Climate Patterns in California." *International Journal of Wildland Fire* 26, no. 4: 253. https://doi.org/10.1071/wf16102.

Keeley, J. E., and A. D. Syphard. 2019. "Twenty-First Century California, USA, Wildfires: Fuel-Dominated vs. Wind-Dominated Fires." *Fire Ecology* 15: 24.

Keeley, J. E., and P. H. Zedler. 1978. "Reproduction of Chaparral Shrubs After Fire: A Comparison of Sprouting and Seeding Strategies." *American Midland Naturalist* 99: 142–161.

Keith, D. A., H. R. Akçakaya, W. Thuiller, et al. 2008. "Predicting Extinction Risks Under Climate Change: Coupling Stochastic Population Models With Dynamic Bioclimatic Habitat Models." *Biology Letters* 4: 560–563.

Kelley, A. E., and M. L. Goulden. 2008. "Rapid Shifts in Plant Distribution With Recent Climate Change." *Proceedings of the National Academy of Sciences of the United States of America* 105: 11823011826.

Kueppers, L. M., M. A. Snyder, L. C. Sloan, E. S. Zavaleta, and B. Fulfrost. 2005. "Modeled Regional Climate Change and California Endemic Oak Ranges." *Proceedings of the National Academy of Sciences of the United States of America* 102: 16281–16286.

Lanner, R. M. 1983. *Trees of the Great Basin: A Natural History*, 215. University of Nevada Press.

Lawson, D. M., H. M. Regan, P. H. Zedler, and J. Franklin. 2010. "Cumulative Effects of Land Use, Altered Fire Regime and Climate Change on Persistence of *Ceanothus verrucosus*, a Rare, Fire-Dependent Plant Species." *Global Change Biology* 16: 2518–2529.

Le Squin, A., I. Boulangeat, and D. Gravel. 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.

Lee-Yaw, J. A., J. L. McCune, S. Pironon, and S. N. Sheth. 2022. "Species Distribution Models Rarely Predict the Biology of Real Populations." *Ecography* 6: e05877.

Legras, E. C., S. B. Vander Wall, and D. I. Board. 2010. "The Role of Germination Microsite in the Establishment of Sugar Pine and Jeffrey Pine Seedlings." *Forest Ecology and Management* 260: 806–813.

Loarie, S. C., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. "The Velocity of Climate Change." *Nature* 462: 1052–1055.

14724642, 2025, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70067, Wiley Online Library on [21/08/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Madsen-Hepp, T. R., J. Franklin, S. McFaul, L. Schauer, and M. J. Spasojevic. 2023. "Plant Functional Traits Predict Heterogeneous Distributional Shifts in Response to Climate Change." *Functional Ecology* 37: 1449–1462.

Maloney, P. E., D. R. Vogler, A. J. Eckert, C. E. Jensen, and D. B. Neale. 2011. "Population Biology of Sugar Pine (*Pinus lambertiana* Dougl.) With Reference to Historical Disturbances in the Lake Tahoe Basin: Implications for Restoration." *Forest Ecology and Management* 262: 770–779.

McIntyre, P. J., J. H. Thorne, C. R. Dolanc, et al. 2015. "Twentieth-Century Shifts in Forest Structure in California: Denser Forests, Smaller Trees, and Increased Dominance of Oaks." *Proceedings of the National Academy of Sciences of the United States of America* 112: 1458–1463.

Merow, C., A. M. Latimer, A. M. Wilson, S. M. McMahon, A. G. Rebelo, and J. A. Silander Jr. 2014. "On Using Integral Projection Models to Generate Demographically Driven Predictions of Species' Distributions: Development and Validation Using Sparse Data." *Ecography* 37: 1167–1183.

Monnier-Corbel, A., A. Robert, Y. Hingrat, B. M. Benito, and A.-C. Monnet. 2023. "Species Distribution Models Predict Abundance and Its Temporal Variation in a Steppe Bird Population." *Global Ecology and Conservation* 43: e02442.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Da Fonseca, and J. Kent. 2000. "Biodiversity Hotspots for Conservation Priorities." *Nature* 403: 853–858.

Nolan, R. H., L. Collins, A. Leigh, et al. 2021. "Limits to Post-Fire Vegetation Recovery Under Climate Change." *Plant, Cell & Environment* 44: 3471–3489.

Overpeck, J. T., and B. Udall. 2020. "Climate Change and the Aridification of North America." *Proceedings of the National Academy of Sciences of the United States of America* 117: 11856–11858.

Pagel, J., and F. M. Schurr. 2011. "Forecasting Species Ranges by Statistical Estimation of Ecological Niches and Spatial Population Dynamics." *Global Ecology and Biogeography* 21: 293–304.

Parisien, M. A., C. Miller, S. A. Parks, E. R. DeLancey, F. N. Robinne, and M. D. Flannigan. 2016. "The Spatially Varying Influence of Humans on Fire Probability in North America." *Environmental Research Letters* 11: 075005.

Parmesan, C., and M. E. Hanley. 2015. "Plants and Climate Change: Complexities and Surprises." *Annals of Botany* 116, no. 6: 849–864.

Pausas, J. G. 2015. "Bark Thickness and Fire Regime." *Functional Ecology* 29: 315–327.

Pausas, J. G., and J. E. Keeley. 2014. "Evolutionary Ecology of Resprouting and Seeding in Fire-Prone Ecosystems." *New Phytologist* 204: 55–65.

Pausas, J. G., and J. E. Keeley. 2023. "Evolutionary Fire Ecology: An Historical Account and Future Directions." *Bioscience* 73: 602–608.

Pearson, R. G., and T. P. Dawson. 2003. "Predicting the Impacts of Climate Change on the Distribution of Species: Are Bioclimatic Envelope Models Useful?" *Global Ecology and Biogeography* 12: 361–371.

Perret, D. L., M. E. K. Evans, and D. F. Sax. 2024. "A Species' Response to Spatial Climatic Variation Does Not Predict Its Response to Climate Change." *Proceedings of the National Academy of Sciences of the United States of America* 121: e2304404120.

Pierce, D. W., J. F. Kalansky, and D. R. Cayan. 2018. *Climate, Drought, and Sea Level Rise Scenarios for California's Fourth Climate Change Assessment. California's Fourth Climate Change Assessment*. California Energy Commission.

Pironon, S., J. Villellas, W. Thuiller, et al. 2018. "The 'Hutchinsonian Niche' as an Assemblage of Demographic Niches: Implications for Species Geographic Ranges." *Ecography* 41: 1103–1113.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Rapacciuolo, G., S. P. Maher, A. C. Schneider, et al. 2014. "Beyond a Warming Fingerprint: Individualistic Biogeographic Responses to Heterogeneous Climate Change in California." *Global Change Biology* 20: 2841–2855.

Regan, H. M., J. B. Crookston, R. Swab, J. Franklin, and D. M. Lawson. 2010. "Habitat Fragmentation and Altered Fire Regime Create Trade-Offs for an Obligate Seeding Shrub." *Ecology* 91: 1114–1123.

Regan, H. M., A. D. Syphard, J. Franklin, et al. 2012. "Evaluation of Assisted Colonization Strategies Under Global Change for a Rare, Fire-Dependent Plant." *Global Change Biology* 18: 936–947.

Rose, M. B., S. J. E. Velazco, H. M. Regan, and J. Franklin. 2023. "Rarity, Geography, and Plant Exposure to Global Change in the California Floristic Province." *Global Ecology and Biogeography* 32: 218–232.

Schwartz, M. W., and A. D. Syphard. 2021. "Fitting the Solutions to the Problems in Managing Extreme Wildfire in California." *Environmental Research Communications* 3: 81005.

Serra-Diaz, J. M., J. Franklin, W. W. Dillon, A. D. Syphard, F. W. Davis, and R. K. Meentemeyer. 2016. "California Forests Show Early Indications of Both Range Shifts and Local Persistence Under Climate Change." *Global Ecology and Biogeography* 25, no. 2: 164–175. https://doi.org/10.1111/geb.12396.

Serra-Diaz, J. M., J. Franklin, M. Ninyerola, et al. 2014. "Bioclimatic Velocity: The Pace of Species Exposure to Climate Change." *Diversity and Distributions* 20: 69–180.

Sofaer, H. R., C. S. Jarnevich, I. S. Pearse, et al. 2019. "Development and Delivery of Species Distribution Models to Inform Decision-Making." *Bioscience* 69: 544–557.

Stephenson, N. 1998. "Actual Evapotranspiration and Deficit: Biologically Meaningful Correlates of Vegetation Distribution Across Spatial Scales." *Journal of Biogeography* 25: 855–870.

Sudworth, G. B. 1908. *Forest Trees of the Pacific Slope*. Government Printing Office.

Swab, R. M., H. M. Regan, D. Matthies, U. Becker, and H. H. Bruun. 2015. "The Role of Demography, Intraspecies Variation, and Species Distribution Models in Species' Projections Under Climate Change." *Ecography* 38: 221–230.

Syphard, A. D., T. J. Brennan, and J. E. Keeley. 2019. "Extent and Drivers of Vegetation Type Conversion in Southern California Chaparral." *Ecosphere* 10: e02796.

Syphard, A. D., T. J. Brennan, H. Rustigian-Romsos, and J. E. Keeley. 2022. "Fire-Driven Vegetation Type Conversion in Southern California." *Ecological Applications* 32: e2626.

Syphard, A. D., V. C. Radeloff, T. J. Hawbaker, and S. I. Stewart. 2009. "Conservation Threats due to Human-Caused Increases in Fire Frequency in Mediterranean-Climate Ecosystems." *Conservation Biology* 23: 758–769.

Syphard, A. D., V. C. Radeloff, J. E. Keeley, et al. 2007. "Human Influence on California Fire Regimes." *Ecological Applications* 17: 1388–1402.

Syphard, A. D., H. M. Regan, J. Franklin, R. M. Swab, and T. C. Bonebrake. 2013. "Does Functional Type Vulnerability to Multiple Threats Depend on Spatial Context in Mediterranean-Climate Regions?" *Diversity and Distributions* 19: 1263–1274.

Syphard, A. D., S. J. E. Velazco, M. B. Rose, J. Franklin, and H. Regan. 2024. "The Importance of Geography in Forecasting Future Fire Patterns Under Climate Change." *Proceedings of the National Academy of Sciences of the United States of America* 121, no. 32: e2310076121.

Theobald, D. M. 2005. "Spatially Explicit Regional Growth Model (SERGOM) v2 Methodology. Report for Trust for Public Lands."

14724642, 2025, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.70067, Wiley Online Library on [21/08/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Thuiller, W., C. H. Albert, A. Dubuis, C. Randin, and A. Guisan. 2010. "Variation in Habitat Suitability Does Not Always Relate to Variation in Species' Plant Functional Traits." *Biology Letters* 6: 120–123.

Thuiller, W., T. Münkemüller, K. H. Chiffers, et al. 2014. "Does Probability of Occurrence Relate to Population Dynamics?" *Ecography* 37: 1–12.

Tyler, C. M., B. Kuhn, and F. W. Davis. 2006. "Demography and Recruitment Limitations of Three Oak Species in California." *Quarterly Review of Biology* 81: 127–152.

Underwood, E. C., J. H. Viers, K. R. Klausmeyer, R. L. Cox, and M. R. Shaw. 2009. "Threats and Biodiversity in the Mediterranean Biome." *Diversity and Distributions* 15: 188–197.

Urban, M. C. 2024. "Climate Change Extinctions." *Science* 386: 1123–1128.

Urban, M. C., P. L. Zarnetske, and D. K. Skelly. 2013. "Moving Forward: Dispersal and Species Interactions Determine Biotic Responses to Climate Change." *Annals of the New York Academy of Sciences* 1297: 44–60.

van Mantgem, P. J., and N. L. Stephenson. 2005. "The Accuracy of Matrix Population Model Projections for Coniferous Trees in the Sierra Nevada, California." *Journal of Ecology* 93: 737–747.

VanDerWal, J., L. P. Shoo, C. N. Johnson, and S. E. Williams. 2009. "Abundance and the Environmental Niche: Environmental Suitability Estimated From Niche Models Predicts the Upper Limit of Local Abundance." *American Naturalist* 174: 282–291.

Velazco, S. J., M. B. Rose, A. F. de Andrade, I. Minoli, and J. Franklin. 2022. "Flexsdm: An R Package for Supporting a Comprehensive and Flexible Species Distribution Modelling Workflow." *Methods in Ecology and Evolution* 13: 1661–1669.

Villero, D., M. Pla, D. Camps, J. Ruiz-Olmo, and L. Brotons. 2017. "Integrating Species Distribution Modelling Into Decision-Making to Inform Conservation Actions." *Biodiversity and Conservation* 26: 251–271.

Warren, R., J. Price, E. Graham, N. Forstenhaeusler, and J. Vanderwal. 2018. "The Projected Effect on Insects, Vertebrates, and Plants of Limiting Global Warming to 1.5°C Rather Than 2°C." *Science* 360: 791–795.

Weber, M. M., R. D. Stevens, J. A. F. Diniz-Filho, and C. E. V. Grelle. 2017. "Is There a Correlation Between Abundance and Environmental Suitability Derived From Ecological Niche Modelling? A Meta-Analysis." *Ecography* 40: 817–828.

Westerling, A. L., and B. P. Bryant. 2008. "Climate Change and Wildfire in California." *Climatic Change* 87: 231–249.

Wolf, A., N. B. Zimmerman, W. R. Anderegg, P. E. Busby, and J. Christensen. 2016. "Altitudinal Shifts of the Native and Introduced Flora of California in the Context of 20th-Century Warming." *Global Ecology and Biogeography* 25: 418–429.

Yang, J., P. J. Weisberg, T. E. Dilts, et al. 2015. "Predicting Wildfire Occurrence Distribution With Spatial Point Process Models and Its Uncertainty Assessment: A Case Study in the Lake Tahoe Basin, USA." *International Journal of Wildland Fire* 24: 380–390.

Zammit, C. A., and P. H. Zedler. 1993. "Size Structure and Seed Production in Even-Aged Populations of *Ceanothus greggii* in Mixed Chaparral." *Journal of Ecology* 81: 499–511.

Zhu, K., C. W. Woodall, and J. S. Clark. 2012. "Failure to Migrate: Lack of Tree Range Expansion in Response to Climate Change." *Global Change Biology* 18: 1042–1052.

Zurell, D., W. Thuiller, J. Pagel, et al. 2016. "Benchmarking Novel Approaches for Modelling Species Range Dynamics." *Global Change Biology* 22: 2651–2664.

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