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RESEARCH ARTICLE

Climate change is associated with a higher extinction risk of a subshrub in anthropogenic landscapes

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Abstract

1. In most ecosystems, the increasingly strong effects of climate change on biodiversity co-occur with other anthropogenic pressures, most importantly land-use change. However, many long-term demographic studies focus on populations monitored in protected areas, and our understanding of how climate change will affect population persistence under anthropogenic land use is still limited.
2. To fill this knowledge gap, we assessed the consequences of co-occurring land-use and climate change on vital rates and population dynamics of a fire-adapted Mediterranean carnivorous subshrub, the dewy pine (*Drosophyllum lusitanicum*). We used 7 years of individual data on 4753 plants monitored in three natural heathland sites that experience primarily fire as a disturbance, and five anthropogenic sites, where fires have been replaced by persistent disturbances from browsing or mechanical vegetation removal as a consequence of land-use change. All sites are projected to experience increasingly hotter summers and drier falls and winters. We used generalised additive models to model non-linear responses of survival, growth and reproduction to rainfall, temperature, size, density and time since fire in anthropogenic and natural dewy-pine populations. We then projected population dynamics under climate-change scenarios using an individual-based model.
3. Our findings reveal that vital rates respond differently to climate change in anthropogenic compared to natural habitats. While extinction risks did not change under climate change in natural habitats, future higher summer temperatures decreased survival and led to population declines and higher extinction probabilities in anthropogenic habitats.
4. *Synthesis*. Our results highlight the possible dramatic effects of climate change on populations largely confined to chronically disturbed, anthropogenic habitats and provide a foundation for devising relevant management strategies aiming towards the protection of species in human-disturbed habitats of the Mediterranean habitat. Overall, our findings emphasize the need for more long-term studies in managed landscapes.

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KEYWORDS
anthropogenic landscape, climate change, disturbance regime, fire adaptation, land-use change, Mediterranean habitat, plant population and community dynamics, population persistence

1 | INTRODUCTION

Land-use change has been identified as the most important driver of biodiversity declines in most ecosystems (Díaz et al., 2019; IPBES, 2019; Sala et al., 2000). Across the globe, human expansion has caused habitat loss and fragmentation through the modification of lands for urbanization or agricultural purposes (Foley et al., 2005), with dire consequences on local and regional species persistence (Selwood et al., 2015) and cascading effects at the community and ecosystem levels (Alberti, 2015; Garnier et al., 2007; Kampichler et al., 2012). Meanwhile, the effects of land-use change on species are increasingly compounded by more severe impacts of climate change on natural systems (Brook et al., 2008; Mantyka-Pringle et al., 2012; Oliver & Morecroft, 2014).

The complex interplay of land-use and climate change is reshaping ecosystems at an unprecedented rate, with profound implications for the persistence of many species (Pereira et al., 2024). Nonetheless, many studies assess the persistence of populations under climate change in protected areas (Murali et al., 2022)—which are generally sheltered from anthropogenic land use and habitat loss (Geldmann et al., 2013; Watson et al., 2014; but see Clark et al., 2013), and where populations are thus overall doing better than those outside protected regions (Geldmann et al., 2013; Gray et al., 2016). This means that, in many studies, the key role of land-use change in shaping the response of populations to changes in climate is omitted (Titeux et al., 2016). Land-use and climate change can have reciprocal effects on each other, leading to non-additive effects of these pressures on populations and communities (Brook et al., 2008; Mantyka-Pringle et al., 2012; Montràs-Janer et al., 2024; Oliver & Morecroft, 2014). Thus, the effects of climate change might differ among land use types, and the consequences of land-use change could depend on the strength of climate change (Mantyka-Pringle et al., 2012). Understanding these dynamics beyond the confines of protected areas is crucial for devising effective conservation strategies.

Land-use, climate change and their interaction (Brook et al., 2008) can affect populations via changes in key vital rates through multiple mechanisms such as inbreeding depression (Bijlsma & Loeschcke, 2012; Leimu et al., 2010), physiological stress (Selwood et al., 2015) or phenotypic selection (Alberti, 2015). Negative effects of climate change on survival could be exacerbated by anthropogenic land use, as habitat fragmentation could hamper individual dispersal, thereby preventing populations from shifting their habitat range to respond to the new conditions arising under climate change (Lawson et al., 2010; Oliver & Morecroft, 2014). Additionally, negative correlations between adaptations to land use and to climate change could cause the selection for the tolerance of one pressure to reduce the capacity to adapt to the other (Chevin et al., 2010; Oliver & Morecroft, 2014). As population sizes decrease, these detrimental effects could be amplified through demographic stochasticity and inbreeding depression (Fagan & Holmes, 2006), as a decrease in genetic variability and its subsequent fitness reduction would lower the capacity of individuals to cope with challenging environmental conditions (Bijlsma & Loeschcke, 2012; Leimu et al., 2010). Nonetheless, in the face of the prevalence of negative effects of both anthropogenic land use and climate change, and given their interacting effects on demographic parameters (Brook et al., 2008; Titeux et al., 2016) and biodiversity (Montràs-Janer et al., 2024), exhaustively assessing population persistence under changing climatic conditions requires studying populations in anthropogenic landscapes.

Mediterranean biomes are among the most sensitive to interacting pressures derived from land use and climate change (Newbold et al., 2020). In these ecosystems, fire is a recurrent disturbance that has shaped plant traits over evolutionary time (Keeley et al., 2012) and is essential to the functioning of ecosystems (Pausas & Bond, 2020). However, many fire-adapted plant species in the Mediterranean Basin are now largely found in anthropized habitats where fire regimes have been substantially altered or suppressed altogether by changes in land use (Ojeda, 2020; Pausas & Keeley, 2014), which can have strong impacts on plant population dynamics (Paniw, Quintana-Ascencio, et al., 2017) and wider ecosystem processes, such as nutrient cycling (Pausas & Bond, 2020). Mediterranean plant populations are also increasingly exposed to shorter and drier winters and hotter summers, jeopardizing the persistence of shrubland communities (Paniw et al., 2021). While the effects of human activities in fire-disturbed habitats on plant population persistence have previously been studied (e.g. Paniw, Quintana-Ascencio, et al., 2017), we still lack a full understanding of population dynamics under the interacting pressures of land use and climate change.

Here, we use a Mediterranean, fire-adapted subshrub, the dewy pine (*Drosophyllum lusitanicum*), as a case study to investigate the effects of changing climatic conditions on population dynamics in natural and anthropogenic habitats. We used 7 years of individual-based data, collected as part of long-term demographic monitoring (since 2011) in natural and anthropogenic (i.e. highly human-dominated permanently disturbed sites) habitats, to parameterize vital-rate responses to interacting climate (temperature and rainfall) and biotic (plant size and intraspecific density) drivers and project resulting population dynamics under climate-change scenarios. We expected higher extinction probabilities in anthropogenic habitats under current climatic conditions, as previous research has shown human disturbances to have a negative effect on population dynamics (Conquet et al., 2023; Paniw, Quintana-Ascencio, et al., 2017), and such disturbances are likely to persist in Mediterranean heathlands

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(Ojeda, 2020). Additionally, given the negative effects of compound anthropogenic pressures on natural systems (Zscheischler et al., 2018), we expected sharper declines in anthropogenic populations than in natural ones under climate change.

2 | METHODS

2.1 | Study species

2.1.1 | Life history

The dewy pine, *Drosophyllum lusitanicum* (Drosophyllaceae), is a rare carnivorous subshrub endemic to the western end of the Mediterranean basin and tightly associated with fire-prone Mediterranean heathlands of southern Spain, Portugal and northern Morocco (Correia & Freitas, 2002; Garrido et al., 2003; Paniw et al., 2015). As with many species in fire-prone habitats, dewy pines have adapted their life history to persist under recurring fire regimes that remove all above-ground vegetation. Populations rely on a persistent soil seedbank (Figure 1), whose dynamics strongly vary with time since fire (TSF_t, where t is the number of years after a fire; Paniw, Quintana-Ascencio, et al., 2017; Conquet et al., 2023). When a fire occurs (TSF_0), the combined effect of heat and vegetation and litter removal triggers the germination of the major part of seeds stored in the seedbank (Figure 1; Appendix S1: Table S1; Cross et al., 2017; Paniw, Quintana-Ascencio, et al., 2017; Gómez-González et al., 2018). Germination from the seedbank continues in later post-fire years but greatly decreases from TSF_2. New seedlings mostly grow during the first year after a fire (TSF_1) and become reproductive plants from the second year after the population burned (TSF_2; Figure 1). The majority of seeds produced by these individuals do not germinate directly but go to the soil seedbank to replenish the population at the next fire (Figure 1). This occurs because dewy pines are increasingly overgrown by dominant shrub vegetation, which hinders seed germination (Gómez-González et al., 2018) and insect prey capture (Paniw et al., 2018), drastically decreasing the survival of above-ground plants after TSF_4 (Paniw et al., 2015).

Despite being fire-adapted, active fire suppression and general degradation of heathland habitats under land-use change (for instance through vegetation removal for wide firebreaks or pine afforestations) mean that most populations of dewy pines as well as numerous other heathland species persist in highly and permanently human-disturbed (hereafter anthropogenic) habitats (Paniw et al., 2015) (see Appendix S2: Table S1 for details on study populations). In such habitats, periodic mechanical clearing of vegetation or browsing—of surrounding vegetation but not on dewy pines—and trampling by domestic ungulates act as a constant disturbance resembling the effect of fire by the removal of above-ground vegetation, but lasting much longer. This has led to important changes in the demographic processes of dewy pines (Conquet et al., 2023; Paniw, Quintana-Ascencio, et al., 2017). Seedbanks in chronically disturbed, anthropogenic populations are likely depleted because the long-term clearance of vegetation means that relatively more seeds germinate immediately instead of going into the seedbank (Appendix S1: Table S1; Gómez-González et al., 2018). Vital rates of above-ground individuals are affected as well; while juvenile survival rapidly decreases after a fire in natural populations, it remains

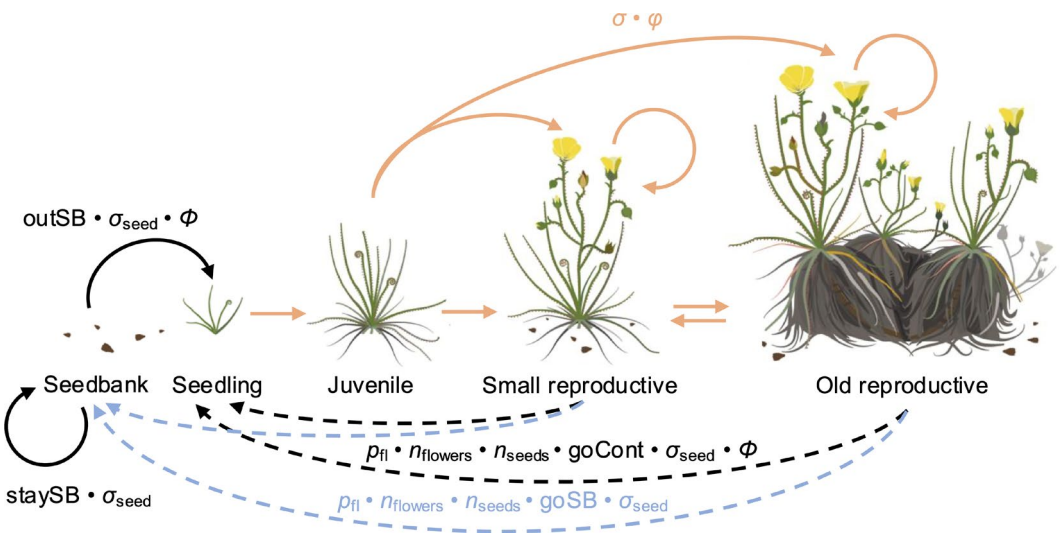


FIGURE 1 Dewy-pine life cycle. Conditional on seed survival (σ_{seed}), seeds in the seedbank germinate, with germination probability outSB, to become seedlings of a given size (Φ) or remain dormant underground (staySB). Above-ground individuals then survive (σ) and grow (φ), depending on their size (size-dependent survival and growth is highlighted in orange); and become reproductive from two years after a fire occurred in natural habitats. Reproductive individuals produce seeds conditional on size-dependent flowering probability (p_{fl}), the number of flowers ($n_{flowers}$) and the number of seeds per flower (n_{seeds}). These seeds, conditional on their survival (σ_{seed}), either germinate directly (goCont; dashed black arrows) and become seedlings of a given size (Φ) or contribute to the underground seedbank (goSB; dashed blue arrow).

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stable over time under human disturbances. However, smaller mature individuals in anthropogenic populations have a lower survival than in natural populations, and reproduction is decreased as well. Moreover, negative density feedbacks are stronger in anthropogenic populations (Conquet et al., 2023).

Anthropogenic pressures in dewy pine habitats are also increasingly interacting with climate change. Temperatures have been increasing in the last four decades (on average by 0.033°C per year) and will continue to do so in the future (Appendix S2: Figures S1 and S2). Contrastingly, while the recent increase in rainfall variability is predicted to reverse, rainfall is forecasted to be less abundant in the future (−0.16 mm per year on average). Such variations in environmental patterns have already been shown to lead to population declines in natural shrublands (Paniw et al., 2023). Dewy pines will therefore likely be increasingly affected by interactions of climate change and human disturbance. Therefore, understanding their response to climate effects will help us discern the joint role of different pressures on plants persisting in anthropogenic habitats.

2.1.2 | Demographic data

We used individual demographic data collected on 4753 dewy pines from eight populations of southern Spain, located in two types of habitats: Mediterranean heathlands experiencing recurrent fire regimes and low levels of anthropogenic pressures such as cattle browsing and trampling (natural populations; $n = 3$); and Mediterranean heathlands that have not burned in the past 40 years but where high anthropogenic pressures constantly remove above-ground vegetation (anthropogenic populations; $n = 5$) (Appendix S2: Table S1). In each population, we obtained information on size, reproduction (probability of flowering and number of flowers), and survival from individually marked plants located in 40 1 × 1 m plots; all individuals, including new recruits, in a given plot were marked and censused every spring in the last week of April or first week of May (see Appendix S1 for details). The Andalusian Consejería de Medio Ambiente issued the requisite permits to undertake fieldwork (permit number Rs-33/13).

2.2 | Estimation of seedbank parameters

To parameterize variation among different habitat types in probabilities of seed germination (goCont for seeds germinating without going to the seedbank and outSB for seeds germinating from the seedbank), dormancy (staySB) and transition to the seedbank (goSB) (Figure 1), we used published data from seed-burial and greenhouse germination experiments (Gómez-González et al., 2018; Paniw, Quintana-Ascencio, et al., 2017). Previous research has shown that in natural populations, most produced seeds (97.4%; 95% confidence interval [96.3%–98.4%]) go to the underground seedbank (Appendix S1: Table S1). While 81% [77.4%–85.2%] of the seeds germinate from the seedbank right after a fire (TSF_0), that proportion greatly decreases in later post-fire habitat stages (6.09% [4.44%–7.75%] in TSF_1 and 3.47% [2.31%–4.63%] in later TSFs). In contrast, in chronically disturbed, anthropogenic populations, a much lower proportion of the produced seeds goes to the seedbank (82.2% [65.3%–97.5%]). In these populations, although 59.8% [56.6%–63.0%] of the underground seeds remain underground, seedbanks are depleted due to the decreased proportion of seeds produced by above-ground plants entering dormancy.

2.3 | Estimation of above-ground vital rates

We investigated how rainfall, temperature and density affect the survival, growth and reproduction of individuals, for natural and anthropogenic dewy-pine populations separately (Appendix S2: Table S1). We used Generalised Additive Models—fitted with the *gam* function of the mgcv package (Wood, 2011, 2017; Wood et al., 2016)—to estimate (1) survival (σ) and flowering probability (p_{fl}) (using a binomial distribution), (2) the number of flowers per individual ($n_{flowers}$; using a negative binomial distribution instead of a simple Poisson model as the data were overdispersed) and (3) growth (φ) and seedling size (Φ), with size = log(number of leaves × length of the longest leaf (cm)) (Figure 1; Paniw, Quintana-Ascencio, et al., 2017). We modelled the latter two vital rates using a scaled *t* distribution ('scat' in the family parameter of the *gam* function) instead of a Gaussian distribution to accommodate the heavy-tailed nature of the response variables (see Appendix S1: Table S4). We tested for the non-linear responses of all vital rates to lag cumulative rainfall and average daily maximum temperature, and above-ground density of large (i.e. size >4.5) intraspecific neighbours. In addition, to account for effects of post-fire habitat stages, we tested for non-linear effects of time since fire (TSF) on vital rates of natural populations. We used a cubic spline basis with three dimensions ($k = 3$) for all these covariates (except for the size effect on the number of flowers, where we used $k = 4$ to model a decline in the number of flowers of large individuals as has been observed in all populations), and a gamma value of 1.4, as is commonly used to reduce the risk of overfitting (Wood, 2017). We also included random year and population effects on the model intercept in all models using a random-effect spline. We performed all analyses in R 4.2.2 via RStudio (Posit Team, 2023; R Core Team, 2022).

2.3.1 | Vital-rate responses to climatic variables (cumulative rainfall and average maximum daily temperature)

We chose rainfall and maximum temperatures as climatic predictors based on recent publications showing the importance of these two drivers on vital rates of Mediterranean plants (García-Callejas

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et al., 2017; Paniw et al., 2023) and based on our a priori expectations given the biology of the study species (Appendix S1: Table S2). We extracted daily rainfall and maximum temperature data with a resolution of 0.1 degree for all dewy-pine population locations from the E-OBS dataset from the EU-FP6 project UERRA and the Copernicus Climate Change Service (Cornes et al., 2018; see Appendix S2 for details). We obtained the monthly cumulative rainfall and average maximum temperature in each population by averaging the values recorded within a buffer of 0.1 × 1.5 degrees (i.e. 1.5 times the grid resolution) around the population coordinates. We assessed the presence of rainfall and temperature lag effects on dewy-pine vital rates using GAMs including cumulative rainfall and average maximum daily temperature across several biologically relevant periods. We defined these periods based on prior knowledge of seasonal climatic effects in Mediterranean shrublands (Paniw et al., 2023; Appendix S1: Table S2); and did not use a sliding-window approach to assess lagged effects to avoid spurious correlations (Evers et al., 2021). For survival and growth, we assessed the effect of climate following the annual population census (set to the 1st of May), while for reproductive parameters (i.e. flowering probability, number of flowers and seedling size), we assessed the effect of climate in periods prior to the census. More specifically, we considered the effect of post-census average maximum temperature in summer (May–September) and of cumulative rainfall in fall (September–November), winter (January–April) or both (September–April), on survival and growth. We tested for the effect of pre-census average maximum daily temperature in winter (January–April), and of cumulative rainfall in fall (September–November) and winter (January–April) on reproductive rates. We considered that the effects of longer lag periods are effectively absorbed by changes in plant size.

2.3.2 | Vital-rate responses to large above-ground individual density

To understand how intraspecific interactions affect dewy-pine vital rates, we included in our models the density of above-ground individuals, specific to a 1-m^2 quadrat in a given population. This spatial resolution matches the study design—where plants are censused in four transects of ten 1-m^2 quadrats (Paniw, Quintana-Ascencio, et al., 2017)—and corresponds to the observed scale at which the plant–plant interactions affecting the demography of dewy pines occur. We only considered individuals of size >4.5, which corresponds to the minimum observed size of reproductive plants. Smaller plants are largely seedlings that have relatively weak effects on plant vital rates, as large individuals are unlikely to be affected by small plants and small plants are primarily affected by large shrubs (Brewer et al., 2021). We did not use a spatially explicit formulation of density dependence (e.g. using the crowding approach described in Adler et al., 2010), as such an approach requires knowledge of the spatial distribution of individuals and seeds, which we lacked for some sites and years.

2.3.3 | Vital-rate model selection

We selected the best vital-rate models using the Akaike information criterion (AIC, using a threshold of ΔAIC >2 to identify a model as performing better than another; Burnham et al., 2011; Wood, 2017) and the number of degrees of freedom. Prior to model selection, we standardized and checked for correlations between all covariates (see Appendix S1 for more details). We first selected the best lag period for the effect of rainfall and temperature and then added—in a forward selection framework—density and size to the model selection and, for natural populations, time since last fire (Appendix S1: Table S3 for more details). We considered two-way interactions among the climatic variables, density, size and TSF as well as site-specific random slopes (e.g. site-specific effects of density or size) in our model selection, using random-effect splines.

2.4 | Population projections under climate change scenarios

2.4.1 | Individual-based model definition

We used the estimated vital rates to parameterize an individual-based model (IBM) and project each natural and anthropogenic dewy-pine population under current and predicted climate conditions. The following is a summary of the IBM specificities; a more detailed description of the different modules of the projection model following the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006, 2020) can be found in Appendix S3. We performed 500 30-year projections of each dewy-pine population under two scenarios: (1) a control scenario corresponding to current climatic conditions where 30 years—and the corresponding rainfall and temperature values—were sampled at random among the past observed ones (2016–2021); and (2) two climate-change scenarios where the rainfall and temperature values corresponded to projected climatic conditions from 2021 to 2050 according to the RCP4.5 and RCP8.5 climate-change scenarios (Riahi et al., 2011). The climate-change scenario comprised 11 sets of 500 population projections, each set corresponding to future rainfall and temperature conditions extracted from 11 global circulation models (GCM; Appendix S2: Table S2) from the Coupled Model Intercomparison Project 6 (CMIP6; Eyring et al., 2016; Pascoe et al., 2020; Waliser et al., 2020) available from the Earth System Grid Federation's (ESFG; Petrie et al., 2021) web application accessible at https://aims2.llnl.gov/search. These models have been used in several studies on ecological systems (Paniw et al., 2022; Tredennick et al., 2016) and differ in their parameterization, enabling us to project the dewy-pine populations under a wide range of possible future climatic conditions and thereby reduce bias in our population projections (Sanderson et al., 2015).

Because most GCMs comprised projected rainfall and temperature values beyond the values observed in our populations, we capped these values to the maximum and minimum observed. This approach allowed us to investigate the response of dewy-pine

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populations to substantial increases in the frequency of extreme climatic conditions, rather than changes in absolute rainfall and temperature values.

Each population projection started with a population vector of z-sized individuals from 2021—the last year used to estimate vital rates—and the initial population thus comprised individuals observed in the population in that year. This also applies to the initial rainfall and temperature values, and the above-ground density of large individuals. While we assumed no fire occurred in anthropogenic populations, we simulated a sequence of 30 post-fire habitat stages for each projection of natural populations. The first post-fire state corresponded to the one observed in 2021, and the subsequent ones were determined based on a Markov matrix containing the among-TSF transition probabilities based on a fire frequency of 1/30 representing the stochastic fire regime occurring in natural dewy-pine populations (see Appendix S3 for details; see also Conquet et al., 2023).

We projected each initial population in discrete yearly steps determining which above-ground individuals reproduced, survived and grew, and how many seeds germinated—from the seedbank or directly after reproduction—or entered or remained in the seedbank. Each of these processes was represented by a sub-model within the general IBM. As annual censuses took place during the flowering period (pre-reproductive census), each projected year started with the reproduction sub-model. This sub-model sampled reproductive individuals (0 or 1) based on a binomial distribution parameterized with the estimated mean flowering probability (p_{fl}). If any individual reproduced, its number of flowers was sampled from a negative binomial distribution based on the estimated mean number of flowers per plant ($n_{flowers}$); and the number of seeds per flower (n_{seeds}) was sampled from a Poisson distribution with a mean of 9.8—the average number of seeds per flower used in Paniw, Quintana-Ascencio, et al. (2017). To avoid excessive reproductive values in natural populations, we capped the number of flowers per individual to the maximum observed number of flowers in each population. In natural populations, where fires could occur, the reproduction sub-model was skipped in the first year after fire, as dewy pine adults are killed by fire and post-fire recruits do not reproduce until 2 years after germination.

The reproduction sub-model was followed by the survival and growth sub-model, which sampled the surviving individuals from a binomial distribution based on the mean estimated survival rate, and assigned them a size to which they would grow at the next time step by sampling from a scaled *t* distribution (to accommodate for heavy-tailed size values when fitting the growth model) based on the mean, standard deviation and degrees of freedom of the fitted growth model. Sporadically sampled positive infinite sizes were set to the maximum observed size in the population in the currently projected year, while negative infinite sizes were set to zero.

Finally, at the end of each projected year, the seedbank sub-model sampled seeds from the seedbank that remained dormant or germinated from binomial distributions based on the respective probabilities (staySB and outSB). The seeds that did not survive—that is, neither germinated nor stayed dormant—were removed from the seedbank. The seeds germinating without going through the seedbank were sampled from a binomial distribution based on the probability of continuous germination (goCont). Some seedbank processes are hidden processes that cannot be easily determined in the field without perturbing the populations. To reduce the resulting bias, we applied a correction factor representing seed survival (σ_{seed}) to the seedbank parameters in anthropogenic populations (see Appendix S1 and Paniw, Quintana-Ascencio, et al. (2017) for more details), and further corrected outSB and goCont in Sierra Carbonera Disturbed by reducing them to 40% of their values. We also capped the number of recruits to the maximum number of seedlings observed in all natural populations as well as in two anthropogenic populations: Bujeo and Sierra Carbonera Disturbed. Ultimately, all recruits were assigned a size by sampling from a scaled *t* distribution based on the estimated mean seedling size as well as its standard deviation and degrees of freedom.

At the end of a projected year, we updated the size of individuals that grew during the previous year as well as the above-ground density for each 1-m^2 quadrat in the population. We also calculated and recorded the annual population growth rate (annual log λ), which we used to calculate the stochastic growth rate log λ_S for each projection (see Appendix S3 for more details; see also Conquet et al., 2023). In each projection, the population was considered extinct if it went below the quasi-extinction threshold set at 5 above-ground individuals and 50 seeds in the seedbank.

2.4.2 | Model validation

We calibrated our vital-rate and individual-based models by projecting each dewy-pine population from the year it was first censused to 2022. We then compared observed and projected above-ground population sizes and population growth rates, as well as individual size distributions across time. For natural populations, we used the observed post-fire habitat stages and did not simulate fire frequencies. This process enabled us to validate our IBM by assessing its ability to well represent the dynamics of the dewy-pine populations in years that were not used in the model-fitting part of our analysis (i.e. years before 2016 when available and 2022).

2.4.3 | Sensitivity analyses

We assessed which demographic rates contribute most to changes in population dynamics under climate change in anthropogenic and natural populations. To do so, we repeated climate-change projections, as described in the previous section, for each population, but we changed climatic drivers under the RCP 8.5 climate-change

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scenario in specific vital rate models only (survival, growth, flowering probability, number of flowers or seedling size), while assuming current climatic conditions in the remaining vital rates. We performed 100 30-year projections and calculated sensitivities as:

$$\text{Sensitivity} = \frac{\sum_{i=1}^{n=100} \left(\log \lambda_{S_perturbed_i} - \log \lambda_{S_control_i}\right) / \log \lambda_{S_control_i}}{n},$$

where i = one of 100 log λ_S, and log $\lambda_{S_control}$ represent population dynamics assuming current climatic conditions in all vital rates. We calculated 500 sensitivity values for each population by randomly sampling 100 log $\lambda_{S_control}$ from the 500 available and comparing them to the 100 available log $\lambda_{S_perturbed}$.

3 | RESULTS

3.1 | Vital-rate responses to habitat disturbance

Dewy-pine vital rates varied between natural and anthropogenic habitats (Figure 2). Survival was on average higher in anthropogenic (mean = 0.42 and 95% confidence interval = [0.18, 0.70]) than in natural habitats (0.27 [0.17, 0.40]; Figure 2). In contrast, we found the opposite pattern for growth (i.e. plant size at $t+1$), which was higher in natural (size 5.0 [4.7, 5.2] at the next time step, calculated as log(number of leaves × length of the longest leaf (cm))) than in anthropogenic sites (4.7 [4.4, 4.9]), as well as flowering probability

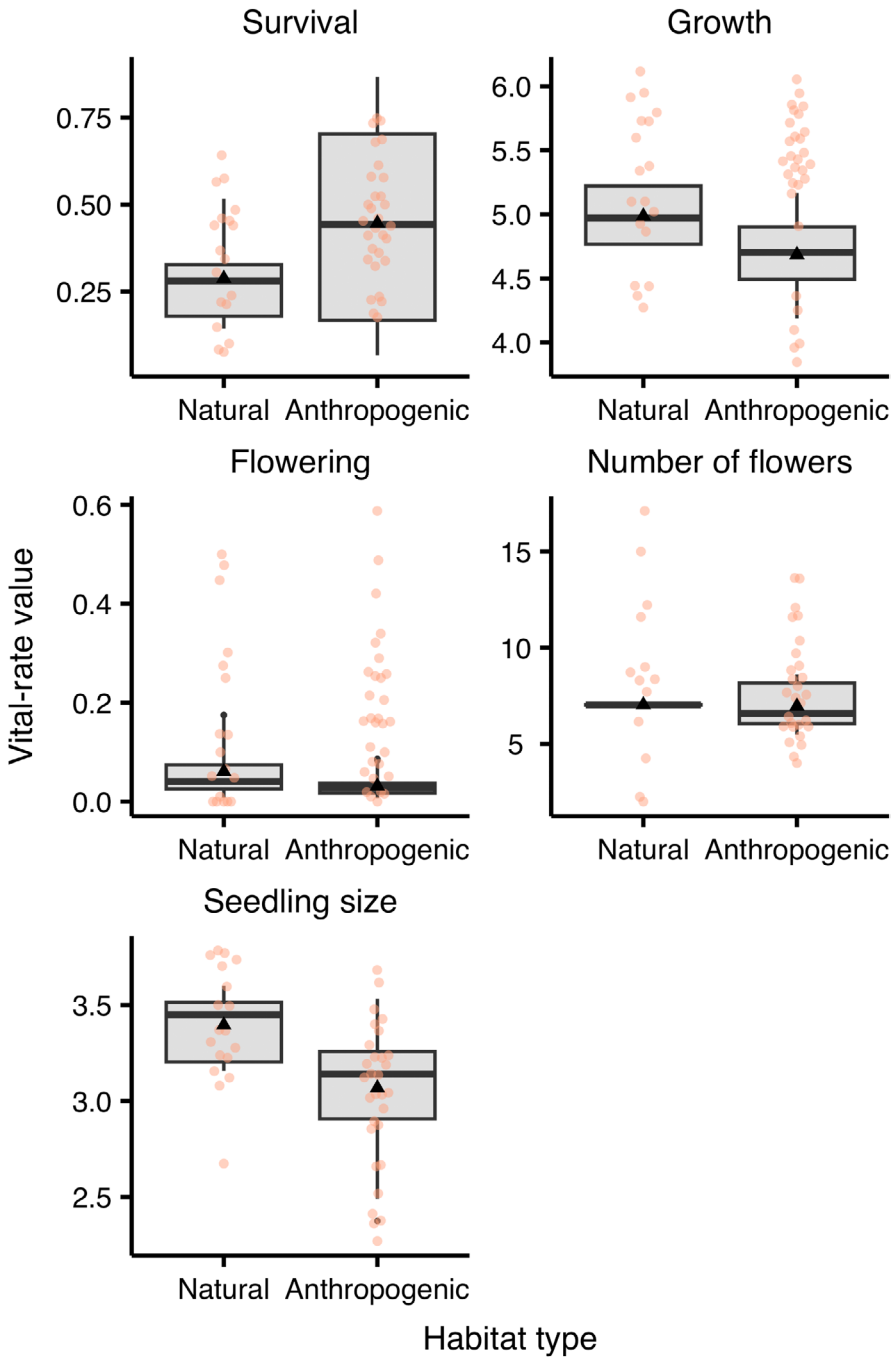


FIGURE 2 Predicted and observed average vital-rate values in natural and anthropogenic populations. The boxplots represent the distribution of the predicted average values of habitat-specific survival, growth, that is, log(number of leaves × length of the longest leaf (cm)), and flowering rates, as well as the number of flowers and seedling size estimated for each population and year from GAMs. The whiskers represent the 2.5th and 97.5th percentiles and the black triangle the mean estimate. We kept covariates at their mean values (scaled value = 0) except for the number of flowers, where we used the mean size of reproducing individuals. The coloured dots represent the observed average vital rates in each population and year.

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(0.039 [0.013, 0.11] in natural and 0.025 [0.013, 0.045] in anthropogenic populations), and seedling size (3.4 [3.2, 3.5] and 3.0 [2.8, 3.3], respectively; Figure 2). However, there was no difference between habitat types in the number of flowers per individual (6.9 [6.2, 7.7] on average in natural populations and 6.7 [5.8, 7.8] in anthropogenic populations; Figure 2). Notably, we found more among-site variation in anthropogenic than in natural conditions, possibly because the level of anthropogenic disturbance differed between sites (Appendix S1: Figure S3).

3.2 | Vital-rate responses to climatic variables

In both anthropogenic and natural habitats, the variation of most vital rates was associated with changes in at least one of the two climatic variables considered in our analysis: monthly cumulative rainfall (hereafter rainfall) or monthly average daily maximum temperature (hereafter temperature) (Figure 3; Appendix S1: Table S4). Most vital rates were more strongly associated with the same climatic variable in the same period of the year in both

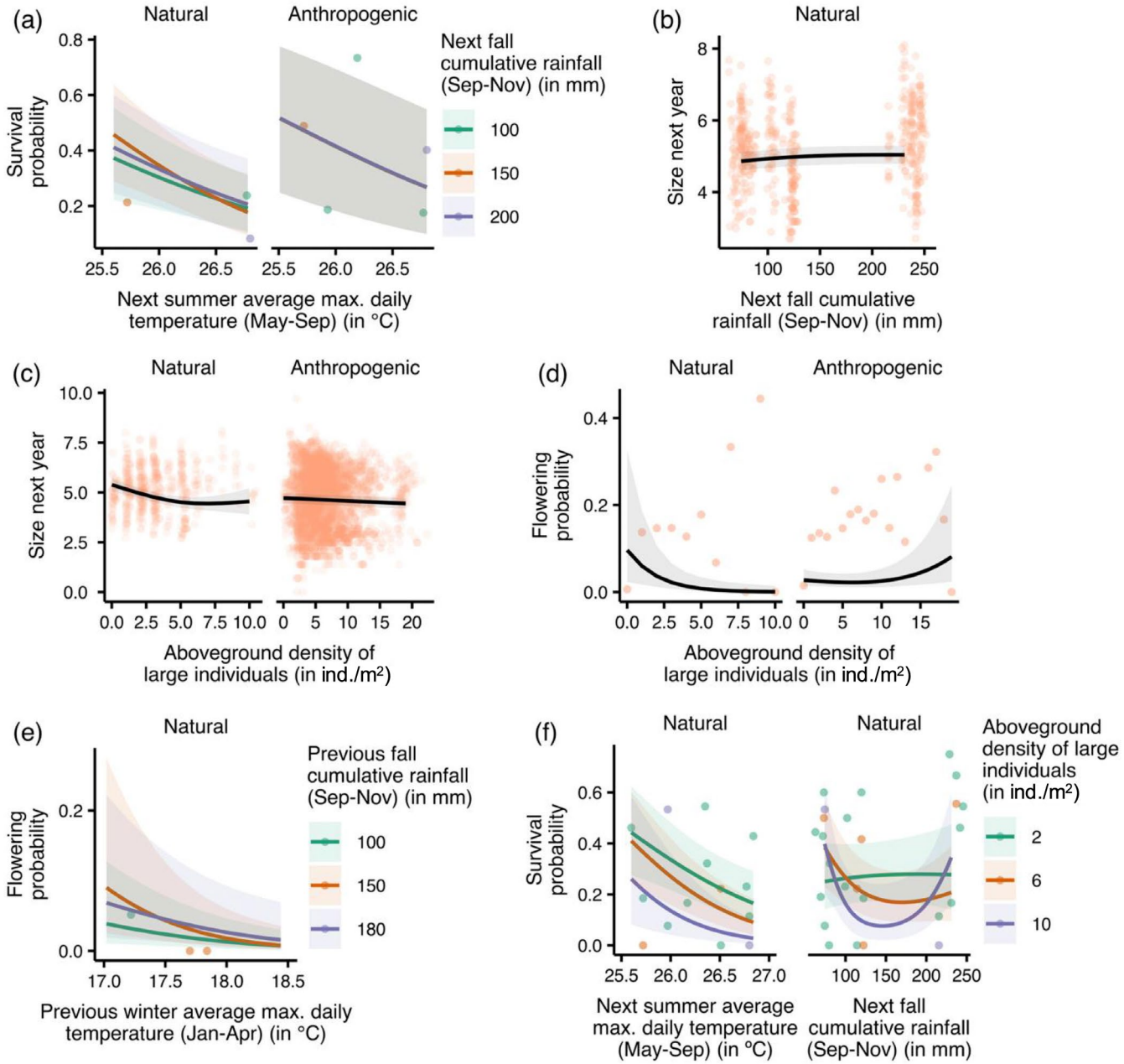


FIGURE 3 Relationships between dewy-pine vital rates and climatic variables and above-ground density of large individuals. Predictions from the GAM models show variation in (a) survival with changes in next summer temperature and next fall rainfall, growth, that is, size (log[number of leaves x length of the longest leaf (cm)]) at $t+1$, with changes in (b) next fall rainfall and (c) aboveground density of large individuals (size >4.5), flowering probability with changes in (d) aboveground density and (e) previous winter temperature and previous fall rainfall, and (f) survival probability with changes in next summer temperature, next fall rainfall, and aboveground density. Lines show the mean predicted vital-rate values and shaded areas the associated 95% confidence interval. Dots represent the observed vital-rate values.

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habitats (e.g. variation in survival was associated with changes in summer temperatures and fall rainfall in both natural and anthropogenic populations). Overall, larger variations in vital rates were associated with changes in temperature than with rainfall (Figure 3; Appendix S1: Table S4).

In both natural and anthropogenic populations, survival was the only vital rate for which variation was associated with changes in both rainfall and temperature (i.e. the fixed effects of both climatic variables were retained in the model selection). With all other covariates held constant at their average value in the respective habitat types, survival was negatively associated with an increase in summer temperatures (i.e. average maximum daily temperature from May to September) (Figure 3a). For example, when temperature increased from 25.5°C to 26.5°C, the average survival rate decreased from 0.47 [0.29, 0.66] to 0.23 [0.14, 0.35] in natural populations, and from 0.51 [0.24, 0.78] to 0.31 [0.12, 0.60] under anthropogenic conditions. In both habitats, variation in survival was also associated with changes in the amount of rainfall in fall (i.e. September–November; Figure 3a; Appendix S1: Table S4 and Figure S4a). In natural populations, this association was on average positive (from 0.25 [0.14, 0.39] under 80 mm of rain to 0.28 [0.16, 0.45] under 200 mm). In contrast, in anthropogenic populations, average survival across sites did not change with rainfall, but investigating this relationship at the site level revealed important among-population variability, with positive associations in some sites (e.g. from 0.39 [0.16, 0.67] under 80 mm of rain to 0.46 [0.21, 0.74] under 200 mm in Sierra del Retín Disturbed) and negative associations in others (e.g. from 0.46 [0.21, 0.74] to 0.36 [0.15, 0.65] in Prisioneros; Appendix S1: Figure S4a). Such among-site differences were almost ubiquitous across vital rates in anthropogenic populations (Appendix S1: Figure S4), but not in natural habitats. For example, on average across all natural sites, individuals grew more with higher amounts of rainfall. More specifically, the longest leaf of an average-sized individual grew from 4.3 to 4.9 [4.6, 5.1] in a year under 80 mm of rain but to 5.0 [4.8, 5.3] under 200 mm (Figure 3b).

3.3 | Vital-rate responses to above-ground density of large plants

In both anthropogenic and natural habitats, plants grew less when densities of large individuals increased (Figure 3c). Under human disturbance, an average-sized individual grew from 4.1 to 4.7 [4.4, 4.9] in a year with 2 large individuals/m^2 but to 4.6 [4.3, 4.8] with 10 ind./m^2 (Figure 3c). In natural conditions, an individual grew from 4.3 to 5.0 [4.7, 5.2] with a density of 2 ind./m^2 but only to 4.6 [3.9, 5.2] with 10 ind./m^2 (Figure 3c). Seedling size also decreased with higher numbers of large individuals above-ground (Appendix S1: Figure S5a). Interestingly, the direction of the association between density and flowering probability differed between habitat types, as the flowering rate was positively associated with density in anthropogenic populations (from 0.50 [0.28, 0.72] with 2 ind./m^2 to 0.65 [0.35, 0.86] with 15 ind./m^2), but strongly negatively in natural ones (from 0.68 [0.41, 0.87] with 2 ind./m^2 to 0.10 [0.013, 0.50] with 7 ind./m^2) (Figure 3d).

3.4 | Vital-rate responses to interactions between climate, density, size and post-fire habitat conditions

In natural—but not in anthropogenic—populations, high amounts of rainfall mitigated the strength of the negative association between temperature and survival, which decreased from 0.48 [0.30, 0.67] at 25.5°C to 0.23 [0.14, 0.36] at 26.5°C under 150 mm of rainfall but only from 0.43 [0.26, 0.63] at 25.5°C to 0.25 [0.13, 0.41] at 26.5°C under 200 mm (Figure 3a). We found a similar pattern for the association between previous winter temperatures and flowering probability, which decreased from 0.72 [0.45, 0.89] at 17.5°C to 0.29 [0.076, 0.66] at 18.5°C with 150 mm of rain but only from 0.73 [0.43, 0.90] to 0.46 [0.15, 0.80] with 180 mm (Figure 3e).

Additionally, in natural populations, survival increased with rainfall at low densities (Figure 3f; from 0.26 [0.16, 0.40] to 0.28 [0.16, 0.44] for 100 and 200 mm of rain at 2 ind./m^2); but these variables had a u-shaped relationship at high densities, with the lowest survival rates reached for about 145 mm of rain (e.g. 0.076 [0.021, 0.24] at 10 ind./m^2). The decline in survival with increasing summer temperatures was also weaker at low (e.g. from 0.47 [0.29, 0.66] at 25.5°C to 0.22 [0.14, 0.35] at 26.5°C with 2 ind./m^2) than at high densities (from 0.45 [0.26, 0.65] to 0.14 [0.077, 0.25] with 6 ind./m^2) (Figure 3f). We also found density-dependent variation in flowering probability and growth with rainfall and seedling size with temperature (Appendix S1: Figure S5). Additionally, the strength and direction of the association between survival rates and both rainfall and temperature in natural populations were also size dependent (Appendix S1: Figure S6g,h).

3.5 | Individual-based model

3.5.1 | Population projections

The projections of our individual-based model over the observed period showed that our parameterization enabled us to correctly represent the population-specific pattern of changes in mean annual change in above-ground population size and of population abundance (Figure 4; Appendix S1: Figure S1). Additionally, observed and projected time-varying size distributions were largely overlapping, with a slight bias towards small individuals in some populations (Appendix S1: Figure S2).

Discrepancies between projected and observed population dynamics occurred both at observed abundance peaks and troughs, and this may in part be explained by the fact that the GAMs parameterized to predict vital rates were smoothed to avoid overfitting to extreme data values. This then constrained estimates of population dynamics (Paniw et al., 2021), but, at the same time, did not

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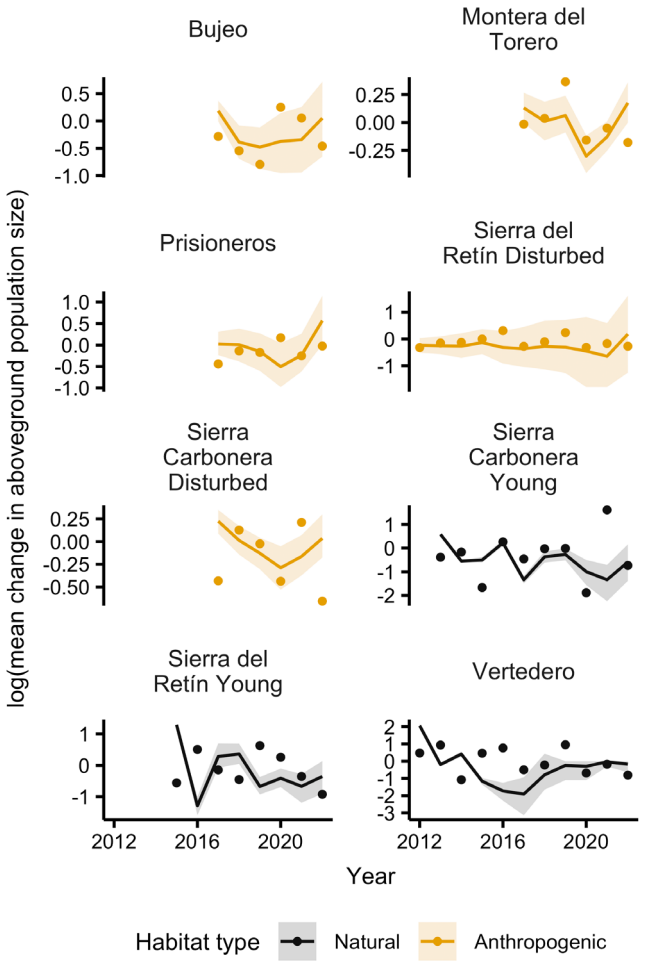


FIGURE 4 Observed and projected average change in above-ground population abundance. We projected each natural and anthropogenic population 500 times across the range of observed years available for each population (maximum range from 2011 to 2022) to perform an out-of-sample validation of our individual-based model parameterization. For each projection, we calculated the log of the average change in above-ground population abundance between years (i.e. $\log(N_t/N_{t-1})$ with N_t the above-ground population size in year t) and obtained the average (line) and 25th and 95th percentiles of the population-specific distribution (shaded ribbon). We compared these projected values to the observed ones (dots).

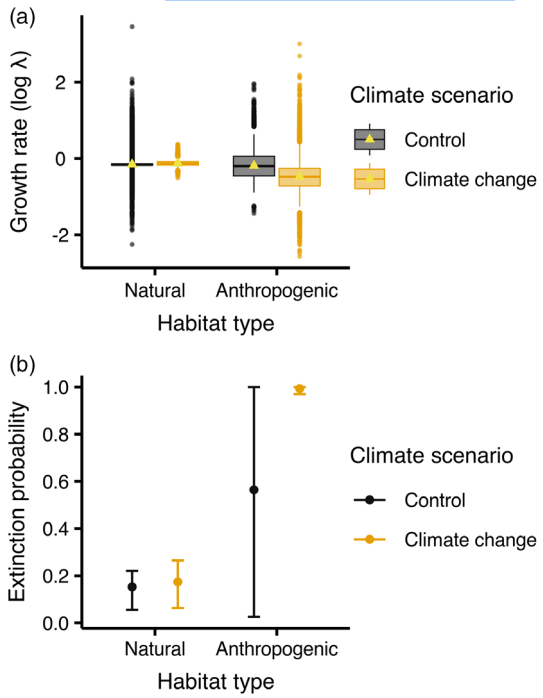


FIGURE 5 Demographic consequences of climate change in natural and anthropogenic populations of dewy pines. We projected each natural and anthropogenic population 500 times for 30 years under a control (keeping temperature and rainfall conditions as currently observed) and two climate-change scenarios (RCP4.5 and RCP8.5). Here, results from scenario RCP8.5 are shown. To assess the demographic consequences of climate change in populations experiencing different levels of human disturbance, we computed for each population: (a) the stochastic population growth rate across 30 years for each population projection (log λ_S; including both the seedbank and above-ground individuals) and (b) the probability of quasi-extinction ($p_{q\text{-}ext}$). Here we summarize these metrics per habitat type, and the variability in the values therefore corresponds to among-population and among-projection differences.

extrapolate the latter beyond biologically realistic values. In addition, discrepancies between projected and observed population dynamics may also occur because our models did not consider (due to a lack of data) other processes that may affect vital rates and thus population dynamics, such as density-dependent germination of seeds from the seedbank or interspecific interactions (Brewer et al., 2021).

Projecting natural and anthropogenic populations under a control scenario (i.e. assuming similar environmental conditions in the future as currently observed) showed that the average population growth rates (log λ_S) did not vary much between habitat types (mean = −0.15, 2.5 and 97.5% quantiles = [−0.62, 0.33] in natural and −0.19 [−0.89, 0.63] in anthropogenic populations; Figure 5). On the other hand, the probability of quasi-extinction ($p_{q\text{-}ext}$) was on average higher in anthropogenic (0.56 [0.026, 1.0]) than in natural populations (0.17 [0.062, 0.26]). Extinction probabilities also varied much more among anthropogenic than among natural populations in the control scenario (Figure 5). In natural populations, the stochastic fire regime in our projections increased the population growth rate substantially after fires, avoiding the quasi-extinction threshold (i.e. 5 above-ground individuals and 50 seeds in the seedbank) in simulations where fires occurred regardless of the population (Conquet et al., 2023). Anthropogenic populations, on the other hand, varied substantially in size, and the high variation in $p_{q\text{-}ext}$ reflects the consistently higher variation in dynamics among populations (Appendix S1: Figure S7).

In contrast with the control scenario, population growth rates differed between habitats under climate change (Figure 5). While the population growth rate (−0.12 [−0.28, 0.072]) and extinction probability (0.17 [0.070, 0.26]) of natural populations did not vary under climate change, under the climate change scenario RCP8.5, our projections show a decrease in log λ_S in anthropogenic sites (−0.47

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[−1.3, 0.45]), accompanied by an increase in the extinction probability (0.99 [0.97, 1.0]) (Figure 5). Results were very similar for scenario RCP4.5 (Appendix S2: Figure S3), highlighting that anthropogenic populations are at a high risk of local extinction even under moderate climate change. In anthropogenic habitats, changes in population dynamics under climate change were largely driven by the adverse effects of climate change on plant survival (Appendix S4: Figures S1 and S2). In natural habitats, climate change effects on survival and growth increased log λ_S in some populations, likely through compensatory density feedbacks, and only climate change effects on reproduction resulted in consistent decreases in log λ_S compared to the control scenario (Appendix S4: Figures S1 and S2).

4 | DISCUSSION

Our individual-based models projecting natural and anthropogenic populations of dewy pines using habitat-specific survival, growth and reproductive rates revealed that the current decline of anthropogenic populations will worsen under climate change, leading to increased extinction risk. While the increasing frequency of extreme high summer temperatures affected both natural and anthropogenic populations negatively, occasionally high rainfall and compensatory density dependence greatly reduced this effect in natural populations. Under chronic, anthropogenic disturbance, however, the decline in survival was not compensated by either of these factors. Consequently, with the frequency of extreme climatic conditions increasing under climate change, populations in anthropogenic habitats—which are currently already decreasing—were negatively affected by future climatic conditions. Habitat dynamics shaped by fires also dominated the effects of environmental perturbations in natural habitats, highlighting the importance of fire regimes in Mediterranean heathlands (Ojeda et al., 2010; Keeley et al., 2011). Adaptations to anthropogenic disturbances meanwhile can lead to changes in vital-rate responses to climate and density, with detrimental consequences on population persistence. The implications of our findings extend beyond ecological theory, offering tangible guidance for conservation policies. Under contrasting responses of natural and anthropogenic populations to climate change, management would need to be adapted to allow periodic vegetation clearance (most importantly through burning) in heathlands which would provoke mass germination from the seed bank of dewy pines and other seeder species, increasing local biodiversity (Fernandes et al., 2013; Ojeda, 2020). In anthropogenic habitats, on the other hand, further disturbances should be prevented (Lawson et al., 2010). As our results highlight climate changes drive population dynamics through adverse effects on survival in anthropogenic habitats, management should focus on improving the survival of large plants, for instance by allowing for moderate shrub cover that shields dewy pines from climatic extremes (Brewer et al., 2021).

Land-use change (e.g. grazing) often has stronger effects on populations than climate change (Sirami et al., 2017). However, few studies assess how interactions between these two environmental pressures affect different vital rates and how such effects then scale to population dynamics, despite evidence of land-use change mediating the effect of climate change on species abundance and diversity (Mantyka-Pringle et al., 2012; Oliver & Morecroft, 2014). Such interactions are likely to be strong drivers of vital-rate responses in habitats such as Mediterranean heathlands, which are among the ecosystems most affected by climate and land-use change (Newbold et al., 2020), the latter leading to changes in disturbance regimes in the habitats. Consequently, interactions between these two pressures might have strong effects on systems such as the dewy pine, where we observe differences among disturbance levels in vital-rate responses to climate, density, and their interactions among natural and highly disturbed habitats.

Our projections of natural and anthropogenic dewy-pine populations under climate change indicate that future changes in climate will spare populations in natural habitats but will have adverse effects on populations experiencing anthropogenic disturbances, which is the majority of dewy pine populations (Garrido et al., 2003), as well as many other Mediterranean shrublands (Newbold et al., 2020). We also note that we capped the effects of projected climate extremes to the maximum past observed values in order to not project population dynamics outside the observed range of responses to climate (Fronzek et al., 2010). However, climate-change projections show increases in extreme temperature values that are clearly outside the range of past observed values (Figure S1), indicating that our projections are likely conservative and local extinction risks for this endangered species may be further exacerbated.

As previously observed in our study populations, anthropogenic disturbances not only lead to increased continuous seed germination and decreased seed dormancy (Appendix S1), but also allow aboveground individuals to survive longer in the absence of shrub encroachment (Paniw, Quintana-Ascencio, et al., 2017). Consequently, dewy pines in chronically disturbed, anthropogenic habitats reach higher sizes than those in natural habitats. This is contrary to many studies assessing trait-level consequences of land-use change—and more specifically grazing—on plants. In these studies, plants in grazed sites adapt to this disturbance by shrinking over time to avoid being consumed by herbivores (Fischer et al., 2011; Kerns et al., 2011; Völler et al., 2017). However, with their mucilage-covered leaves, dewy pines are not palatable to herbivores (Ojeda et al., 2021), and therefore do not require such an adaptation. On the contrary, the small amount or absence of damage dealt to plants by herbivores along with the removal of other plants and the subsequent release of both intra- and interspecific competition might allow dewy pines in anthropogenic populations to grow without surrounding vegetation hampering their nutrient acquisition (Paniw et al., 2018) and growth (Grime, 1973; Hjalten et al., 1993; Kambatuku et al., 2011; Figure 3c).

While anthropogenic disturbances allow dewy pine plants to survive and grow better than in natural conditions, this comes at the cost of reproduction, with flowering probability decreasing in the largest individuals. Although the consequences of land-use change on plant reproduction are clearly species- and

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site-dependent (Kerns et al., 2011; Völler et al., 2017), trade-offs similar to those observed in our populations are common across taxa (Stearns, 1989). Such negative correlations between vital rates might be more striking under stressful conditions such as low resource availability (Villellas & García, 2018). This might be the case in anthropogenic populations of dewy pines particularly. Plants rely almost exclusively on capturing prey invertebrates for nutrient uptake (Paniw, Gil-Cabeza, & Ojeda, 2017; Skates et al., 2019). In natural populations, invertebrates, especially insect pollinators, are abundant after fires, when many post-fire ephemeral species flower, and dewy pine plants are more conspicuous to insects, thus facilitating prey capture and nutrient uptake (Paniw et al., 2018). In anthropogenic habitats, intense browsing or mechanical vegetation removal are likely to decrease invertebrate abundances with respect to natural sites (Carpio et al., 2014; Mayer, 2004). When shrub cover is chronically low or sparse, dewy pine plants are more conspicuous to prey insects but they may also be more exposed to wind and solar radiation, thus resulting in relatively more stressful environmental conditions (Paniw et al., 2018). In turn, while populations in these chronically disturbed, anthropogenic habitats appear to persist, a low reproductive output may generate an extinction debt, where the population structure is skewed towards old individuals that cannot be replaced in the long term (Matías et al., 2019).

Adverse disturbance effects on vital rates can be exacerbated under unfavourable climatic conditions (e.g. Hindle et al., 2023; see also Nolan et al., 2021 and references therein). Plants commonly suffer from extreme temperatures and drought, which affect individuals through processes such as heat stress, photosynthesis inhibition or reduced soil moisture and water resources (e.g. Larcher, 2000; McDowell et al., 2008; Nolan et al., 2021). While dewy pines are somewhat adapted to dry and hot summer conditions (Adamec, 2009; Adlassnig et al., 2006; Darwin, 1875), survival greatly decreases with increasing summer temperatures. In addition to the aforementioned processes reducing the survival of plants experiencing high temperatures, such extreme conditions could lead to a great reduction in prey availability. These carnivorous subshrubs indeed rely on droplets of mucilage on their leaves to capture insects, from which they obtain nutrients (Paniw, Gil-Cabeza, & Ojeda, 2017). However, increasing temperatures and the subsequent decrease in humidity could prevent plants from forming these droplets, and thereby from accessing these resources.

Rainfall also played an important role in shaping dewy-pine demography. In addition to limiting water resources (McDowell et al., 2008), extremely low amounts of rain do not provide enough moisture for dewy pines to produce mucilage on their leaf-traps (Adamec, 2009; Adlassnig et al., 2006; Darwin, 1875). As a result, plants might not get enough nutrients to allocate to the different demographic processes. However, in natural populations, high amounts of rainfall seemed to slightly buffer negative temperature effects, likely by compensating for the low humidity and water resources under high temperatures. This process did not seem to occur in anthropogenic populations, where the increased exposure to extreme temperatures due to sparse vegetation cover might be too intense to counterbalance.

In addition to interactions between climatic variables, density-dependent effects of climate are common across taxa and can play a key role in shaping population dynamics, for example by enhancing or mitigating adverse environmental effects (Gamelon et al., 2017; Paniw et al., 2019). In plant populations, vital-rate density dependence can be attributed to two main biological processes: competition (e.g. for light or pollinators; Craine & Dybzinski, 2013) and facilitation (i.e. the positive effect of neighbours on a focal individual, e.g. through shading or protection from herbivory; Callaway & Pugnaire, 2007; Graff et al., 2007; Le Bagousse-Pinguet et al., 2012). According to the stress-gradient hypothesis, variations in environmental conditions can lead to shifts between these two processes in a given population (Bertness & Callaway, 1994; Maestre et al., 2005), for example under increased levels of disturbance (Graff et al., 2007; Le Bagousse-Pinguet et al., 2012; Villarreal-Barajas & Martorell, 2009) or extreme climatic conditions (Callaway & Pugnaire, 2007; Grant et al., 2014; Olsen et al., 2016). This was the case in dewy pines, where intraspecific density had opposite effects on some vital rates between natural—where competition prevailed—and anthropogenic populations—where facilitation was at play.

As commonly observed in plant communities (Adler et al., 2018; Villalobos et al., 2016), increasing intraspecific densities in natural conditions led to declining survival—with the exception of early post-fire conditions, where facilitation generally predominates in fire-adapted plant communities (Paniw et al., 2018; Vilà & Sardans, 1999). For dewy pines, in addition to the more common resources for which plants compete (e.g. light or pollinators), such negative effects of conspecifics on survival could arise from competition for prey (Craine & Dybzinski, 2013). Contrastingly, individuals in anthropogenic populations benefitted from higher intraspecific densities. In addition to the competition release stemming from the removal of surrounding vegetation (Catling et al., 2024), increasing levels of disturbance such as browsing might lead to a shift from competition to facilitation, as neighbours might act as a barrier against browsers (Le Bagousse-Pinguet et al., 2012).

In addition to the consequences on vital rates, future increases in temperatures and decreases in rainfall under climate change are expected to lead to a higher frequency and intensity of wildfires (Nolan et al., 2021; Turco et al., 2019). In populations where land-use change led to seedbank depletions through an increase in continuous germination and dormancy loss, returning fire regimes will likely have strong negative consequences on population persistence, as reduced soil seedbanks will not be enough to replenish populations following the removal of above-ground individuals by fire. A decrease in the ability of fire-adapted plants to germinate or resprout after more frequent and intense fire could have dramatic consequences for the persistence of plant communities in fire-prone habitats (Enright et al., 2015; Nolan et al., 2021).

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Overall, our findings highlight the existence of demographic responses to climate and land-use change and call for conservation policies taking into account the detrimental effects of climate change on populations persisting under human alterations to their habitats, more specifically in fire-adapted systems. Moreover, species-specific effects of interactions between climate and land-use change highlight the need for studies assessing these effects at the community level—accounting for the effects of both climate and intra- and interspecific density—to understand how interactions between these pressures might affect fire-prone and more generally anthropogenic landscapes.

AUTHOR CONTRIBUTIONS

Eva Conquet: Conceptualization; methodology; software; validation; formal analysis; investigation; data curation, writing—original draft; writing—review and editing; visualization. Arpat Ozgul: Conceptualization; methodology; resources; writing—review and editing; supervision; project administration; funding acquisition. Susana Gómez-González: Validation; investigation; resources; writing—review and editing. Fernando Ojeda: Investigation; resources; writing—review and editing; supervision; project administration; funding acquisition. Maria Paniw: Conceptualization; methodology; software; validation; formal analysis; investigation; data curation; writing—original draft; writing—review and editing; supervision; project administration; funding acquisition. Our work was performed in collaboration with scientists based in the country where the study was initiated and carried out. The perspective of locally based authors who have strong experience with the focal system was paramount to ensure our conclusions took into account the local context. Additionally, we relied on literature previously published by scientists from the region.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70150.

DATA AVAILABILITY STATEMENT

The data necessary for reproducing results and graphs presented in this study are available on GitHub (https://github.com/EvaCnqt/DewyPinesLandUseClimateChange) and Zenodo https://doi.org/10.5281/zenodo.16370815 (Conquet et al., 2025). Original data can be requested from Maria Paniw (maria.paniw@ebd.csic.es). Code for formatting data, implementing and running models and analyses, and plotting results is available on GitHub: https://github.com/EvaCnqt/DewyPinesLandUseClimateChange. The version of code used for this study is archived on Zenodo https://doi.org/10.5281/zenodo.16370815 (Conquet et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Methodological details and additional results.

Appendix S2. Current and future rainfall and temperature data in dewy-pine populations.

Appendix S3. Individual-based model description.

Appendix S4. Results from sensitivity analyses.

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