Climate change amplifies extinction risk of a subshrub in anthropogenic landscapes

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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.

Data and Code Availability Statement

The data necessary for reproducing results and graphs presented in this study are available on Zenodo [link] (+ ref). 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 [link] (+ref).

Conflict of Interest Statement

The authors declare no conflict of interest.

Statement on Inclusion

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.

Climate change amplifies extinction risk of a subshrub in anthropogenic landscapes

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 studies of population dynamics 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 population dynamics of a fire-adapted Mediterranean carnivorous subshrub, the dewy pine (*Drosophyllum lusitanicum*). We used seven years of individual data on 4,753 plants monitored in three natural heathland sites that experience primarily fire as a main 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 do not change under climate change in natural habitats, future higher summer temperatures decrease survival and lead 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 emphasise the need for more long-term studies in managed landscapes.

Keywords

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

Introduction

Land-use change has been identified as the most important driver of biodiversity declines in most ecosystems (Sala et al., 2000; Díaz et al., 2019; IPBES, 2019). Across the globe, human expansion has caused habitat loss and fragmentation through the modification of lands for urbanisation or agricultural purposes (Foley et al., 2005), with dire consequences on local and regional species

49 persistence (Selwood et al., 2015) and cascading effects at the community and
50 ecosystem levels (Garnier et al., 2007; Kampichler et al., 2012; Alberti, 2015).
51 Meanwhile, the effects of land-use change on species are increasingly compounded
52 by more severe impacts of climate change on natural systems (Brook et al., 2008;
53 Mantyka-Pringle et al., 2012; Oliver & Morecroft, 2014).
54
55 The complex interplay of land-use and climate change is reshaping ecosystems at
56 an unprecedented rate, with profound implications for the persistence of many
57 species. Nonetheless, many studies assess the persistence of populations under
58 climate change in protected areas (Murali et al., 2022)—which are generally
59 sheltered from anthropogenic land use and habitat loss (Geldmann et al., 2013;
60 Watson et al., 2014; but see Clark et al., 2013), and where populations are thus
61 overall doing better than those outside protected regions (Geldmann et al., 2013;
62 Gray et al., 2016). This means that, in many studies, the key role of land-use change
63 in shaping the response of populations to changes in climate is omitted (Titeux et al.,
64 2016). Land-use and climate change can have reciprocal effects on each other,
65 leading to non-additive effects of these pressures on populations and communities
66 (Brook et al., 2008; Mantyka-Pringle et al., 2012; Oliver & Morecroft, 2014; Montràs-
67 Janer et al., 2024). Thus, the effects of climate change might differ among land use
68 types, and the consequences of land-use change could depend on the strength of
69 climate change (Mantyka-Pringle et al., 2012). Understanding these dynamics
70 beyond the confines of protected areas is crucial for devising effective conservation
71 strategies.
72

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 (Leimu et al., 2010; Bijlsma & Loeschcke, 2012), 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 to shift 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 (Leimu et al., 2010; Bijlsma & Loeschcke, 2012). Nonetheless, in 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). 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 (Pausas & Keeley, 2014), which can have strong impacts on plant population dynamics (Paniw, Quintana-Ascencio et al., 2017). Mediterranean plant populations are also increasingly exposed to shorter and drier winters and hotter summers, jeopardising 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 on 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 seven 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 (Paniw, Quintana-Ascencio et al., 2017; Conquet et al., 2023). 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.

Methods

Study species

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 to fire-prone Mediterranean heathlands of southern Spain, Portugal, and northern Morocco (Correia & Freitas, 2002; Garrido et al., 2003; Paniw et al., 2015). As many species in fire-prone habitats, dewy pines have adapted their life history to persist under recurring fire regimes that remove all aboveground vegetation. Populations rely on a persistent soil seedbank (Fig. 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 trigger the germination of the major part of seeds stored in the seedbank (Fig. 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; Fig. 1). The majority of seeds produced by these

148 individuals do not germinate directly but go to the soil seedbank to replenish the
149 population at the next fire (Fig. 1). This occurs because dewy pines are increasingly
150 overgrown by dominant shrub vegetation, which hinders seed germination (Gómez-
151 González et al., 2018) and insect prey capture (Paniw et al., 2018), drastically
152 decreasing the survival of aboveground plants after TSF_4 (Paniw et al., 2015).
153
154 Despite being fire-adapted, active fire suppression and general degradation of
155 heathland habitats under land-use change (for instance through vegetation removal
156 for wide firebreaks or pine afforestations) mean that most populations of dewy pines
157 as well as numerous other heathland species persist in highly and permanently
158 human-disturbed (hereafter anthropogenic) habitats (Paniw et al., 2015). In such
159 habitats, periodic mechanical clearing of vegetation or browsing—of surrounding
160 vegetation but not on dewy pines—and trampling by domestic ungulates act as a
161 constant disturbance resembling the effect of fire by the removal of aboveground
162 vegetation, but lasting much longer. This has led to important changes in the
163 demographic processes of dewy pines (Paniw, Quintana-Ascencio et al., 2017;
164 Conquet et al., 2023). Seedbanks in chronically disturbed, anthropogenic
165 populations are likely depleted because the long-term clearance of vegetation means
166 that relatively more seeds germinate immediately instead of going into the seedbank
167 (Appendix S1: Table S1; Gómez-González et al., 2018). Vital rates of aboveground
168 individuals are affected as well; while juvenile survival rapidly decreases after a fire
169 in natural populations, it remains stable across time under human disturbances.
170 However, smaller mature individuals in anthropogenic populations have a lower
171 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 ºC per year) and will continue to do so in the future (Appendix S2: Fig. 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 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.

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); and mediterranean heathlands that have not burned in the past 40 years but where high anthropogenic pressures constantly remove aboveground vegetation (anthropogenic populations) (see Appendix S1 for details).

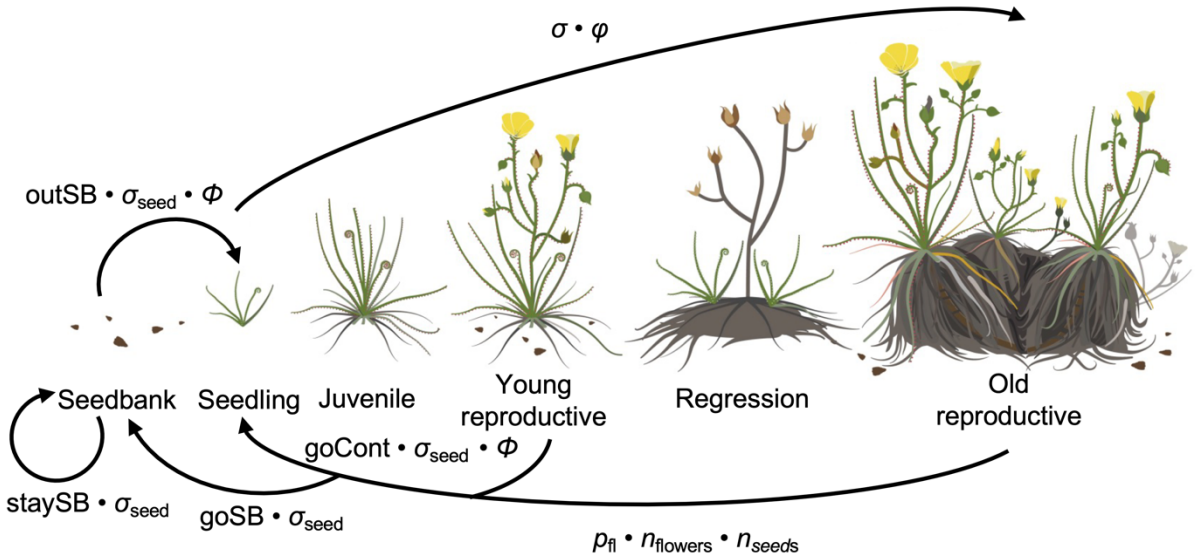


Figure 1 – Dewy-pine life cycle. After a fire, conditional on seed survival (σ_{seed}), seeds in the seedbank germinate to become seedlings of a given size (Φ) conditional on germination probability (outSB), or remain dormant underground (staySB). Individuals then grow conditional on survival and size at the next timestep (σ and φ) and become reproductive from two years after a fire occurred. Reproductive individuals produce seeds conditional on 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) and become seedlings of a given size (Φ) or contribute to the underground seedbank (goSB).

Estimation of seedbank parameters

To quantify the 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) (Fig. 1), we used data

212 from seed-burial and greenhouse germination experiments (Paniw, Quintana-
213 Ascencio et al., 2017; Gómez-González et al., 2018). In natural populations, most
214 produced seeds (97.4%; 95% CI [96.3%–98.4%]) go to the underground seedbank
215 (Appendix S1: Table S1). While 81% [77.4%-85.2%] of the seeds germinate from the
216 seedbank right after a fire (TSF_0), that proportion greatly decreases in later post-fire
217 habitat stages (6.09% [4.44%–7.75%] in TSF_1 and 3.47% [2.31%–4.63%] in later
218 TSFs). In contrast, in chronically disturbed, anthropogenic populations, a much lower
219 proportion of the produced seeds goes to the seedbank (82.2% [65.3%–97.5%]). In
220 these populations, although 59.8% [56.6%–63.0%] of the underground seeds remain
221 underground, seedbanks are depleted due to the decreased proportion of seeds
222 produced by aboveground plants entering dormancy.
223
224 ## Estimation of aboveground vital rates
225
226 We investigated how rainfall, temperature, and density affect the survival, growth,
227 and reproduction of individuals in natural and anthropogenic dewy-pine populations.
228 We used Generalised Additive Models—fitted with the *gam* function of the mgcv
229 package (Wood, 2011; Wood et al., 2016; Wood, 2017)—to estimate (1) survival (σ)
230 and flowering probability (p_{fl}) (using a binomial distribution), (2) the number of flowers
231 per individual ($n_{flowers}$; using a negative binomial distribution), and (3) growth (φ) and
232 seedling size (Φ), with size = log(number of leaves $\times$ length of the longest leaf) (Fig.
233 1; Paniw, Quintana-Ascencio et al., 2017). We modelled the latter two vital rates
234 using a scaled *t* distribution ("scat" in the family parameter of the *gam* function)
235 instead of a Gaussian distribution to accommodate the heavy-tailed nature of the
236 response variables. We tested for the nonlinear responses of all vital rates to lag

cumulative rainfall and average daily maximum temperature, and aboveground density of large (i.e., size > 4.5) intraspecific neighbours. In addition, to account for effects of post-fire habitat stages, we tested for nonlinear 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 in all models using a random-effect spline. We performed all analyses in R 4.2.2 via RStudio (R Core Team, 2022; Posit team, 2023).

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

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. 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.

Vital-rate responses to large aboveground individual density

To understand how intraspecific interactions affect dewy-pine vital rates, we included in our models the density of aboveground 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 which 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.

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 standardised 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 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.

Population projections under climate change scenarios

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

312 the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006; 2020)
313 can be found in Appendix S3. We performed 500 30-year projections of each dewy-
314 pine population under two scenarios: (1) a control scenario corresponding to current
315 climatic conditions where 30 years—and the corresponding rainfall and temperature
316 values—were sampled at random among the past observed ones (2016–2021); and
317 (2) a climate-change scenario where the rainfall and temperature values
318 corresponded to projected climatic conditions from 2021 to 2050 according to the
319 RCP8.5 climate-change scenario (Riahi et al., 2011). The climate-change scenario
320 comprised 11 sets of 500 population projections, each set corresponding to future
321 rainfall and temperature conditions extracted from 11 global circulation models
322 (GCM; Appendix S2: Table S2) from the Coupled Model Intercomparison Project 6
323 (CMIP6; Eyring et al., 2016; Pascoe et al., 2020; Waliser et al., 2020) available from
324 the Earth System Grid Federation's (ESFG; Petrie et al., 2021) web application
325 accessible at https://aims2.llnl.gov/search. These models have been used in several
326 studies on ecological systems (Tredennick et al., 2016; Paniw et al., 2022) and differ
327 in their parameterisation, enabling us to project the dewy-pine populations under a
328 wide range of possible future climatic conditions and thereby reduce bias in our
329 population projections (Sanderson et al., 2015).
330
331 Because most GCMs comprised projected rainfall and temperature values beyond
332 the values observed in our populations, we capped these values to the maximum
333 and minimum observed. This approach, as well as using RCP8.5, which is the most
334 extreme climate-change scenario, allowed us to investigate the response of dewy-
335 pine populations to substantial increases in the frequency of extreme climatic
336 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 aboveground 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 aboveground individuals reproduced, survived, and grew, and how many seeds germinated—from the seedbank or directly after reproduction—or entered or remained in the seedbank. 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 parameterised 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 et al. (2017). To avoid excessive reproductive values in natural populations,

362 we capped the number of flowers per individual to the maximum observed number of
363 flowers in each population. In natural populations, where fires could occur, the
364 reproduction sub-model was skipped in the first year after fire, as dewy pine adults
365 are killed by fire and postfire recruits do not reproduce until two years after
366 germination.
367
368 The reproduction sub-model was followed by the survival and growth sub-model,
369 which sampled the surviving individuals from a binomial distribution based on the
370 mean estimated survival rate, and assigned them a size to which they would grow at
371 the next time step by sampling from a scaled *t* distribution (to accommodate for
372 heavy-tailed size values when fitting the growth model) based on the mean, standard
373 deviation, and degrees of freedom of the fitted growth model. Sporadically sampled
374 positive infinite sizes were set to the maximum observed size in the population in the
375 currently projected year, while negative infinite sizes were set to zero.
376
377 Finally, at the end of each projected year, the seedbank sub-model sampled seeds
378 from the seedbank that remained dormant or germinated from binomial distributions
379 based on the respective probabilities (staySB and outSB). The seeds that did not
380 survive—i.e., neither germinated or stayed dormant—were removed from the
381 seedbank. The seeds germinating without going through the seedbank were
382 sampled from a binomial distribution based on the probability of continuous
383 germination (goCont). Some seedbank processes are hidden processes that cannot
384 be easily determined in the field without perturbing the populations. To reduce the
385 resulting bias, we applied a correction factor representing seed survival (σ_{seed}) to the
386 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 aboveground 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 aboveground individuals and 50 seeds in the seedbank.

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 aboveground 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

411 dynamics of the dewy-pine populations in years that were not used in the model-
412 fitting part of our analysis (i.e., years before 2016 when available, and 2022).
413

414 Results

415

416 Vital-rate responses to habitat disturbance

417

418 Dewy-pine vital rates varied between natural and anthropogenic habitats (Fig.
419 2). Survival was on average higher in anthropogenic (mean = 0.42 and 95%
420 confidence interval = [0.18, 0.70]) than in natural habitats (0.27 [0.17, 0.40]; Fig. 2).
421 In contrast, we found the opposite pattern for growth, which was higher in natural
422 (size 5.0 [4.7, 5.2] at the next time step, calculated as log(number of leaves $\times$ length
423 of the longest leaf)) than in anthropogenic sites (4.7 [4.4, 4.9]), as well as flowering
424 probability (0.039 [0.013, 0.11] in natural and 0.025 [0.013, 0.045] in anthropogenic
425 populations), and seedling size (3.4 [3.2, 3.5] and 3.0 [2.8, 3.3], respectively; Fig. 2).
426 However, there was no difference between habitat types in the number of flowers per
427 individual (6.9 [6.2, 7.7] on average in natural populations and 6.7 [5.8, 7.8] in
428 anthropogenic populations; Fig. 2). Notably, we found more among-site variation in
429 anthropogenic than in natural conditions, possibly because the level of
430 anthropogenic disturbance differed between sites (Appendix S1: Fig. S3).

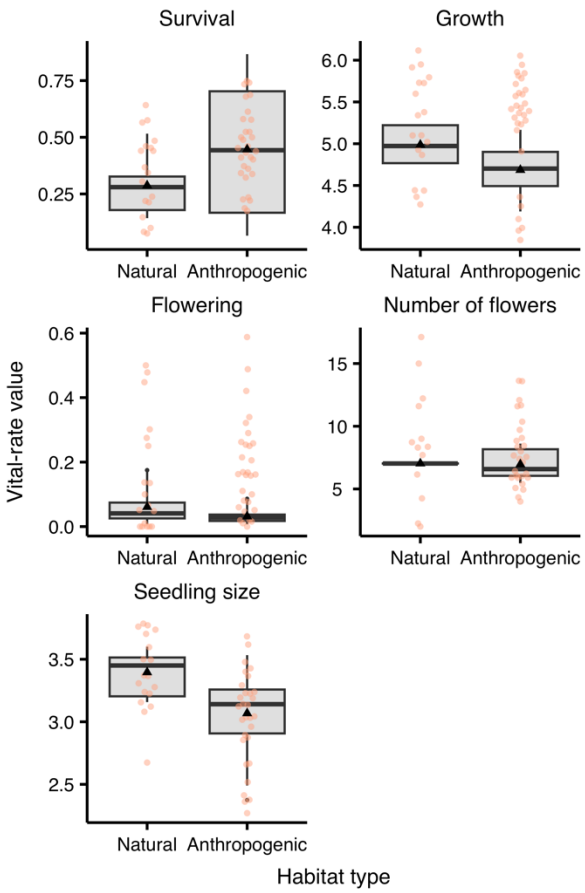
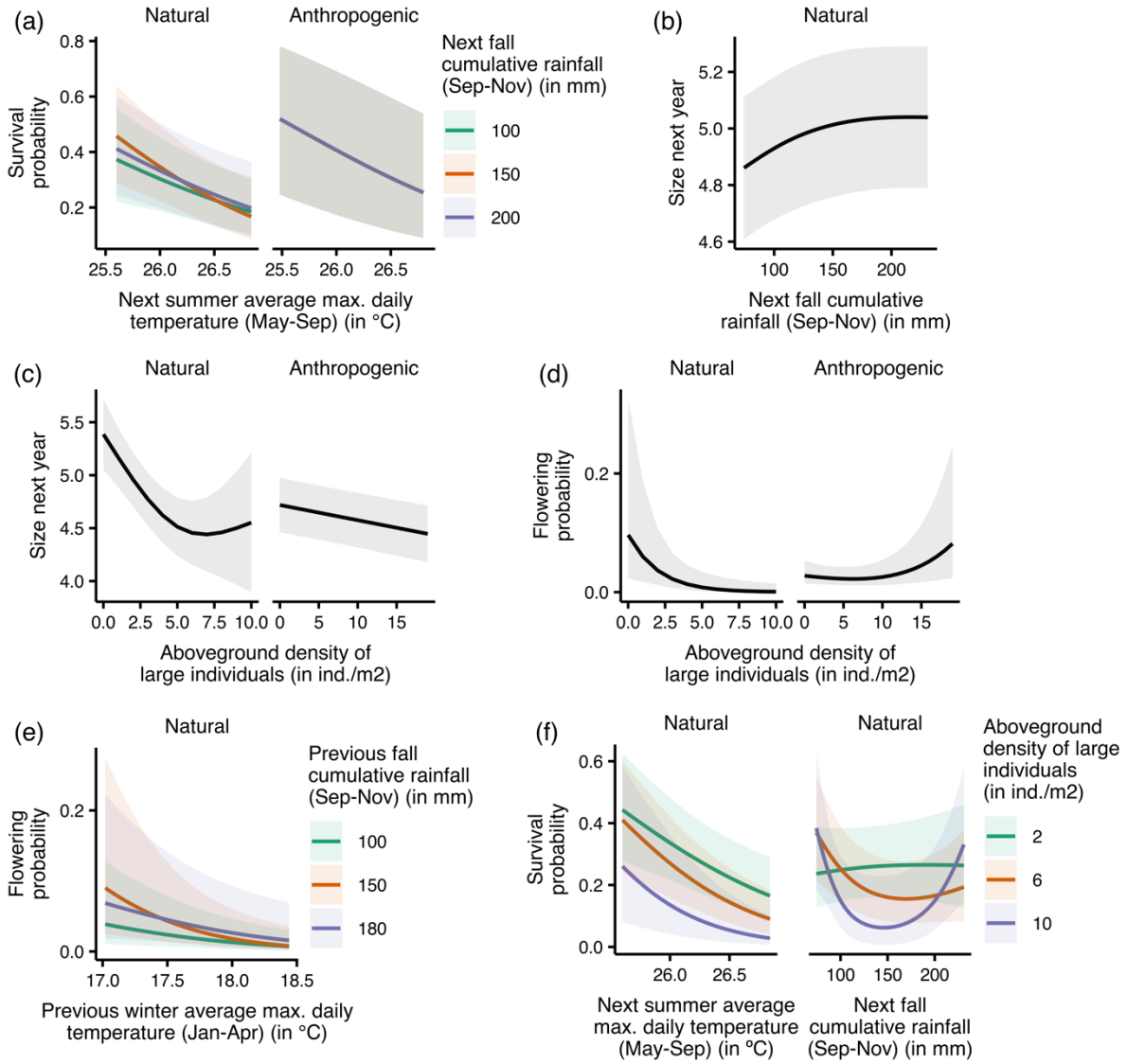


Figure 2 – Predicted and observed average vital-rate values in natural and anthropogenic populations. The boxplots represent the distribution of the predicted average values of habitat-specific survival, growth, and flowering rates, as well as the number of flowers and seedling size estimated for each 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.

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) (Fig. 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 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 (Fig. 3; Appendix S1: Table S4).



462 **Figure 3 – Relationships between dewy-pine vital rates and climatic**
463 **variables and aboveground density of large individuals.** Predictions from the
464 GAM models show variation in (a) survival and (b) flowering probability with changes
465 in temperature (next summer and previous winter, respectively) and rainfall (next and
466 previous fall), (c) flowering probability with changes in previous fall rainfall and
467 density, and growth with (d) changes in next fall rainfall, and (e) aboveground density
468 of large individuals (size > 4.5). Lines show the mean vital-rate values and shaded
469 areas the associated 95% confidence interval.
470

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) (Fig. 3a). For example, when temperature increased from 25.5 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; Fig. 3a, Appendix S1: Table S4 and Fig. 6e). 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: Fig. S3). Such among-site differences were almost ubiquitous across vital rates in anthropogenic populations (Appendix S1: Fig. 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 (Fig. 3b).

Vital-rate responses to aboveground density of large plants

In both anthropogenic and natural habitats, plants grew less when densities of large individuals increased (Fig. 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 (Fig. 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 (Fig. 3c). Seedling size also decreased with higher numbers of large individuals aboveground (Appendix S1: Fig. 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) (Fig. 3d).

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 ºC to 0.23 [0.14, 0.36] at 26.5 ºC under 150 mm of rainfall but only from 0.43 [0.26, 0.63] at 25.5 ºC to 0.25 [0.13, 0.41] at 26.5 ºC under 200 mm (Fig. 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 ºC to 0.29 [0.076, 0.66] at 18.5 ºC with 150 mm of rain but only from 0.73 [0.43, 0.90] to 0.46 [0.15, 0.80] with 180 mm (Fig. 3e).

Additionally, in natural populations, survival increased with rainfall at low densities (Fig. 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./m2); but these variables had a u-shaped relationship at high densities, with lowest survival rates reached for about 145 mm of rain (e.g. 0.076 [0.021, 0.24] at 10 ind./m2). 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./m2) than at high densities (from 0.45 [0.26, 0.65] to 0.14 [0.077, 0.25] with 6 ind./m2) (Fig. 3f). We also found density-dependent variation in flowering probability and growth with rainfall and seedling size with temperature (Appendix S1: Fig. 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: Fig. S6g,h).

Individual Based Model

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 aboveground population size and of population abundance (Fig. 4; Appendix S1: Fig. S1). Additionally, observed

and projected time-varying size distributions were largely overlapping, with a slight bias towards small individuals in some populations (Appendix S1: Fig. S2).

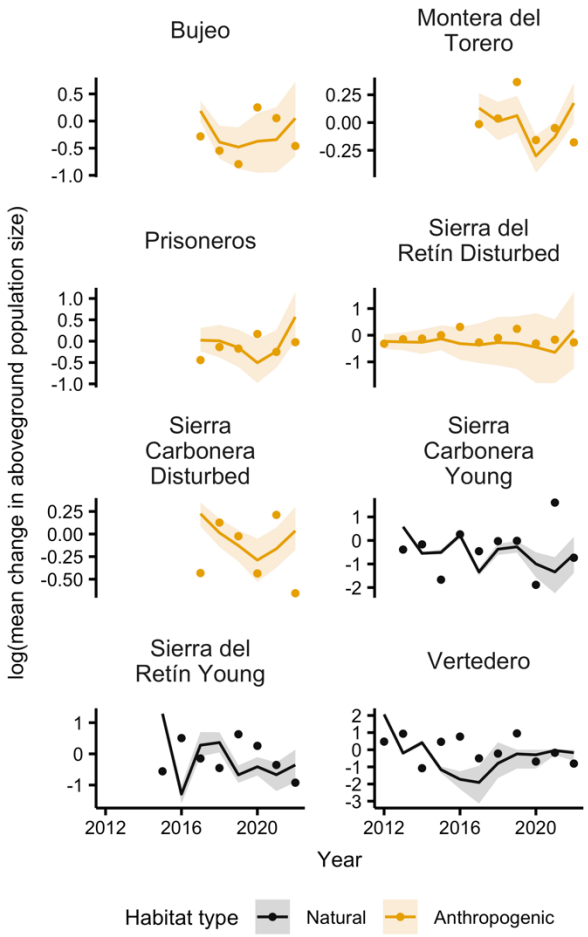


Figure 4 – Observed and projected average change in aboveground population abundance. We projected each natural and anthropogenic population for 500 times across the range of observed years available for each population (maximum range from 2011 to 2022) to perform an out-of-sample validation of our individual-based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

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; Fig. 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 (Fig. 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 aboveground 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: Fig. S7).

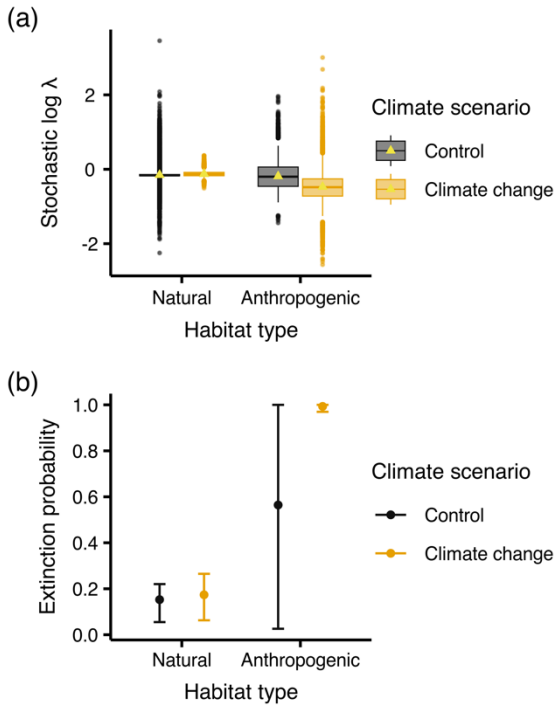


Figure 5 – Demographic consequences of climate change in natural and anthropogenic populations of dewy pines. We projected each natural and anthropogenic population 500 times for 30 years under a control (keeping temperature and rainfall conditions as currently observed) and a climate-change scenario. 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 aboveground individuals) and (b) the probability of quasi-extinction ($p_{q\text{-}ext}$). Here we summarise these metrics per habitat type, and the variability in the values therefore correspond to among-population and among-projection differences.

In contrast with the control scenario, population growth rates differed between habitats under climate change (Fig. 5). While the population growth rate (-0.12 [-

610 0.28, 0.072]) and extinction probability (0.17 [0.070, 0.26]) of natural populations did
611 not vary under climate change, our projections show a decrease in log λ_S in
612 anthropogenic sites (-0.47 [-1.3, 0.45]), accompanied by an increase in the extinction
613 probability (0.99 [0.97, 1.0]).
614

615 ## Discussion

616

617 Our individual-based models projecting natural and anthropogenic populations
618 of dewy pines using habitat-specific survival, growth, and reproductive rates revealed
619 that the current decline of anthropogenic populations will worsen under climate
620 change, leading to increased extinction risk. While the increasing frequency of
621 extreme high summer temperatures affected both natural and anthropogenic
622 populations negatively, occasionally high rainfall and compensatory density
623 dependence greatly reduced this effect in natural populations. Under chronic,
624 anthropogenic disturbance, however, the decline in survival was not compensated by
625 either of these factors. Consequently, with the frequency of extreme climatic
626 conditions increasing under climate change, populations in anthropogenic habitats—
627 which are currently already decreasing—were negatively affected by future climatic
628 conditions. Habitat dynamics shaped by fires also dominated the effects of
629 environmental perturbations in natural habitats, highlighting the importance of fire
630 regimes in Mediterranean heathlands (Ojeda, Pausas, and Verdú, 2010; Keeley et
631 al., 2011). Adaptations to anthropogenic disturbances meanwhile can lead to
632 changes in vital-rate responses to climate and density, with detrimental
633 consequences on population persistence. The implications of our findings extend
634 beyond ecological theory, offering tangible guidance for conservation policies. By

showing the consequences of climate and land-use changes in non-protected habitats, our study provides a foundation for informing relevant stakeholders and developing management strategies that protect biodiversity in the Mediterranean biome, where interacting effects of local and global anthropogenic pressures affect population viability.

Land-use change (e.g. grazing) often has stronger effects on populations than climate change (Sirami et al., 2017). However, few studies assess the consequences of interactions between these two environmental pressures on population dynamics, despite evidence of land-use change mediating the effect of climate change on species abundance and diversity (Mantyka-Pringle, Martin, and Rhodes, 2012; Oliver and Morecroft, 2014). Such interactions are likely to be strong drivers of population dynamics 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 environmental conditions 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).

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 allowed 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 reached 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 adapted 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; Fig. 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 site-dependent (Kerns et al., 2011; Völler et al., 2017), tradeoffs 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 et al., 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 (Mayer, 2004; Carpio et al., 2014). 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 (Darwin 1875; Adlassnig et al., 2006; Adamec, 2009), survival greatly decreased with increasing summer temperatures. In addition

710 to the aforementioned processes reducing the survival of plants experiencing high
711 temperatures, such extreme conditions could lead to a great reduction in prey
712 availability. These carnivorous subshrubs indeed rely on droplets of mucilage on
713 their leaves to capture insects, from which they obtain nutrients (Paniw, Gil-Cabeza
714 et al., 2017). However, increasing temperatures and the subsequent decrease in
715 humidity could prevent plants from forming these droplets, and thereby from
716 accessing these resources.
717
718 Rainfall also played an important role in shaping dewy-pine demography. In addition
719 to limiting water resources (McDowell et al., 2008), extremely low amounts of rain do
720 not provide enough moisture for dewy pines to produce mucilage on their leaf-traps
721 (Darwin 1875; Adlassnig et al., 2006; Adamec, 2009). As a result, plants might not
722 get enough nutrients to allocate to the different demographic processes. However, in
723 natural populations, high amounts of rainfall seemed to slightly buffer negative
724 temperature effects, likely by compensating the low humidity and water resources
725 under high temperatures. This process did not seem to occur in anthropogenic
726 populations, where the increased exposure to extreme temperatures due to sparse
727 vegetation cover might be too intense to counterbalance.
728
729 In addition to interactions between climatic variables, density-dependent effects of
730 climate are common across taxa and can play a key role in shaping population
731 dynamics, for example by enhancing or mitigating adverse environmental effects
732 (Gamelon et al., 2017; Paniw et al., 2019). In plant populations, vital-rate density
733 dependence can be attributed to two main biological processes: competition (e.g. for
734 light or pollinators; Craine & Dybzinski, 2013) and facilitation (i.e., the positive effect

735 of neighbours on a focal individual, e.g., through shading or protection from
736 herbivory; Callaway & Pugnaire, 2007; Graff et al., 2007; Le Bagousse-Pinguet et al.,
737 2012). According to the stress-gradient hypothesis, variations in environmental
738 conditions can lead to shifts between these two processes in a given population
739 (Bertness & Callaway, 1994; Maestre et al., 2005), for example under increased
740 levels of disturbance (Graff et al., 2007; Villarreal-Barajas & Martorell, 2009; Le
741 Bagousse-Pinguet et al., 2012) or extreme climatic conditions (Callaway & Pugnaire,
742 2007; Grant et al., 2014; Olsen et al., 2016). This was the case in dewy pines, where
743 intraspecific density had opposite effects on some vital rates between natural—
744 where competition prevailed—and anthropogenic populations—where facilitation
745 was at play.
746
747 As commonly observed in plant communities (Villalobos et al., 2016; Adler et al.,
748 2018), increasing intraspecific densities in natural conditions led to declining
749 survival—with the exception of early post-fire conditions, where facilitation generally
750 predominates in fire-adapted plant communities (Vilà & Sardans, 1999; Paniw et al.,
751 2018). For dewy pines, in addition to the more common resources for which plants
752 compete (e.g. light or pollinators), such negative effects of conspecifics on survival
753 could arise from competition for prey (Craine & Dybzinski, 2013). Contrastingly,
754 individuals in anthropogenic populations benefited from higher intraspecific densities.
755 In addition to the competition release stemming from the removal of surrounding
756 vegetation (Catling et al., 2024), increasing levels of disturbance such as browsing
757 might lead to a shift from competition to facilitation, as neighbours might act as a
758 barrier against browsers (Le Bagousse-Pinguet et al., 2012).
759

In addition to the consequences on vital rates, future increases in temperatures and decreases in rainfall under climate change are expected to lead to higher frequency and intensity of wildfires (Turco et al., 2019; Nolan et al., 2021). In populations where land-use change led to seedbank depletions through 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 aboveground individuals by fire. 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).

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 inter-specific density—to understand how interactions between these pressures might affect fire-prone and more generally anthropogenic landscapes.

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Appendix S1 – Methodological details and additional results

1. Seedbank parameters

We used previously published data obtained from seed-burial and greenhouse-germination experiments to parameterise the transitions of dewy-pine seeds from and to the soil seedbank and to continuous germination (Table S1). More specifically, following Paniw et al. (2017), we used data on seeds buried in habitat conditions characteristic of early (i.e., recently burned) or late post-fire stages (i.e., long unburned) to estimate seed survival in the soil (i.e., seedbank stasis; staySB) and the probability of germinating from the seedbank at least two years after burial (outSB). We used estimates from recently burned habitats for anthropogenic populations, which experience constant anthropogenic disturbances mimicking the effects of fire (Paniw et al., 2017). For natural populations, we used estimates from burned habitats in early post-fire stages (i.e., TSF_2 for staySB and TSF_1 for outSB), and from unburned habitats in later post-fire stages (i.e., from TSF_3 for staySB and from TSF_2 to TSF_4 for outSB). To more accurately describe the observed seedbank dynamics in the first TSFs (i.e., TSF_0 and TSF_1 for staySB and TSF_0 for outSB), we used previously published parameters representing the characteristically high germination rates from the seedbank (outSB) in a fire year (TSF_0), and low germination rates in late TSFs (TSF_5), as well as the very low seedbank stasis (staySB) following a fire (TSF_0 and TSF_1) (Paniw et al., 2017; Conquet et al., 2023).

To estimate the probability of seeds germinating continuously without contributing to the seedbank (goCont) and its opposite parameter determining the probability of

seeds contributing to the seedbank (goSB), we used data from a growth-chamber germination experiment (see details in Gómez-González et al., 2018). Seeds from 15 individual dewy pines growing in natural or anthropogenic habitats were monitored to obtain the proportion of surviving seeds germinating (goCont) and remaining dormant (goSB = 1 - goCont). We used estimates from the corresponding habitat to parameterise seedbank transitions of our natural and anthropogenic populations. In natural populations, however, continuous germination and contribution to the seedbank only starts in TSF_2 and is extremely low from TSF_5. We therefore fixed the values for goCont and goSB using previously published data (Paniw et al., 2017; Conquet et al., 2023) for these TSFs to represent these observed processes (Table S1). Because natural populations still experience fires, we defined time-since-fire-specific parameter values for these populations. Additionally, to take advantage of the population-specific data available from the germination experiment for several anthropogenic sites, we defined population-specific goCont and goSB values for anthropogenic populations.

Table S1 – Seedbank parameters obtained from seed-burial and germination experiments. We used previously published data from a seed-burial experiment in recently burned and long unburned dewy-pine habitats to estimate the proportion of seeds remaining in (staySB) or germinating from the seedbank (outSB). Additionally, we used data from a germination experiment on seeds from natural and anthropogenic habitats to estimate the proportion of seeds contributing to the seedbank (goSB) or germinating continuously (goCont). The table contains parameter means and, wherever available, 95% confidence intervals (with binomial standard deviations calculated as $\sqrt{\frac{\mu\times(1-\mu)}{N}}$ where μ is the parameter mean and *N* the

sample size). Asterisks indicate parameter values adapted from previously published values (Paniw et al., 2017; Conquet et al., 2023), and for which the confidence interval could not be calculated.

Natural populations				
	Seedbank parameters			
Time since fire (TSF)	staySB	outSB	goCont	goSB
TSF_0	0.1*	0.81*	0*	0*
TSF_1	0.05*	0.061 [0.044, 0.077]	0*	0*
TSF_2	0.60 [0.57, 0.63]	0.035 [0.023, 0.046]	0.026 [0.016, 0.037]	0.97 [0.96, 0.98]
TSF_3	0.85 [0.83, 0.86]	0.035 [0.023, 0.046]	0.026 [0.016, 0.037]	0.97 [0.96, 0.98]
TSF_4	0.85 [0.83, 0.86]	0.035 [0.023, 0.046]	0.026 [0.016, 0.037]	0.97 [0.96, 0.98]
TSF_5	0.85 [0.83, 0.86]	0*	0.01*	0.99*
Anthropogenic populations				
	Seedbank parameters			
Site	staySB	outSB	goCont	goSB
Sierra del Retín Disturbed	0.60 [0.57, 0.63]	0.061 [0.044, 0.077]	0.11 [0, 0.28]	0.89 [0.72, 1.0]
Prisioneros	0.60 [0.57, 0.63]	0.061 [0.044, 0.077]	0.29 [0.0071, 0.57]	0.71 [0.99, 0.43]
Bujeo	0.60 [0.57, 0.63]	0.061 [0.044, 0.077]	0.16 [0.060, 0.26]	0.84 [0.74, 0.94]
Montera del Torero	0.60 [0.57, 0.63]	0.061 [0.044, 0.077]	0.18 [0, 0.37]	0.82 [0.63, 1.0]
Sierra Carbonera Disturbed	0.60 [0.57, 0.63]	0.061 [0.044, 0.077]	0.16 [0.060, 0.26]	0.84 [0.74, 0.94]

2. Seedbank parameters correction factors

Accurately estimating seedbank parameters is complex due to the many factors influencing germination and dormancy. Seed mortality is a hidden process that cannot be easily determined in the field without perturbing the populations and is therefore often underestimated. Therefore, to better represent the dewy-pine population dynamics in anthropogenic sites, we computed a correction factor corresponding to the seed aboveground survival (σ_{seed}). σ_{seed} corresponded to the proportion of seeds surviving aboveground and was obtained from data on flower damage (σ_{seed} = 1 – flower damage) (Paniw et al., 2017). As anthropogenic populations never returned to TSF_0, we only used σ_{seed} for TSF_4 (0.33). We corrected the seedbank parameter values in anthropogenic habitats by multiplying all four seedbank parameters (i.e., goCont, outSB, goSB, and staySB) by σ_{seed}. Additionally, previous model calibrations showed the need to further correct several seedbank parameters to mirror the observed dynamics of dewy-pine populations. To do so, we multiplied both goCont and outSB by 0.4 for Sierra Carbonera Disturbed. Moreover, as we estimated plant density within 1-m^2 quadrats, we avoided unrealistically high recruit numbers by capping the number of recruits to the maximum observed number of seedlings per quadrat during the study period in all natural populations and in two anthropogenic populations: Bujeo and Sierra Carbonera Disturbed. In natural populations, this number was TSF specific; however, data was unavailable for some TSFs in some populations. When unavailable for TSF_0, we set the maximum number of recruits to 1.5 times the maximum observed number of seedlings in the populations; in TSF_1, we set it to the maximum observed number of seedlings in the population; and in TSF_2 to the average maximum observed number of seedlings in the population in $TSF_{>0}$. The

correction factors resulted in predicted abundances (out-of-sample predictions) reflecting well observed abundances, size distributions, and aboveground population growth rates (Fig. S1; Fig. S2; Fig. 4 in main text).

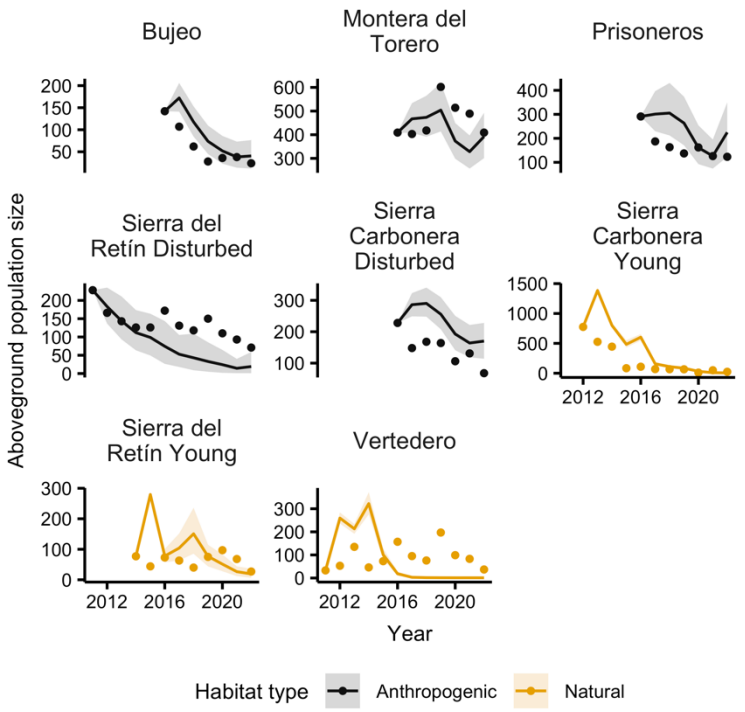
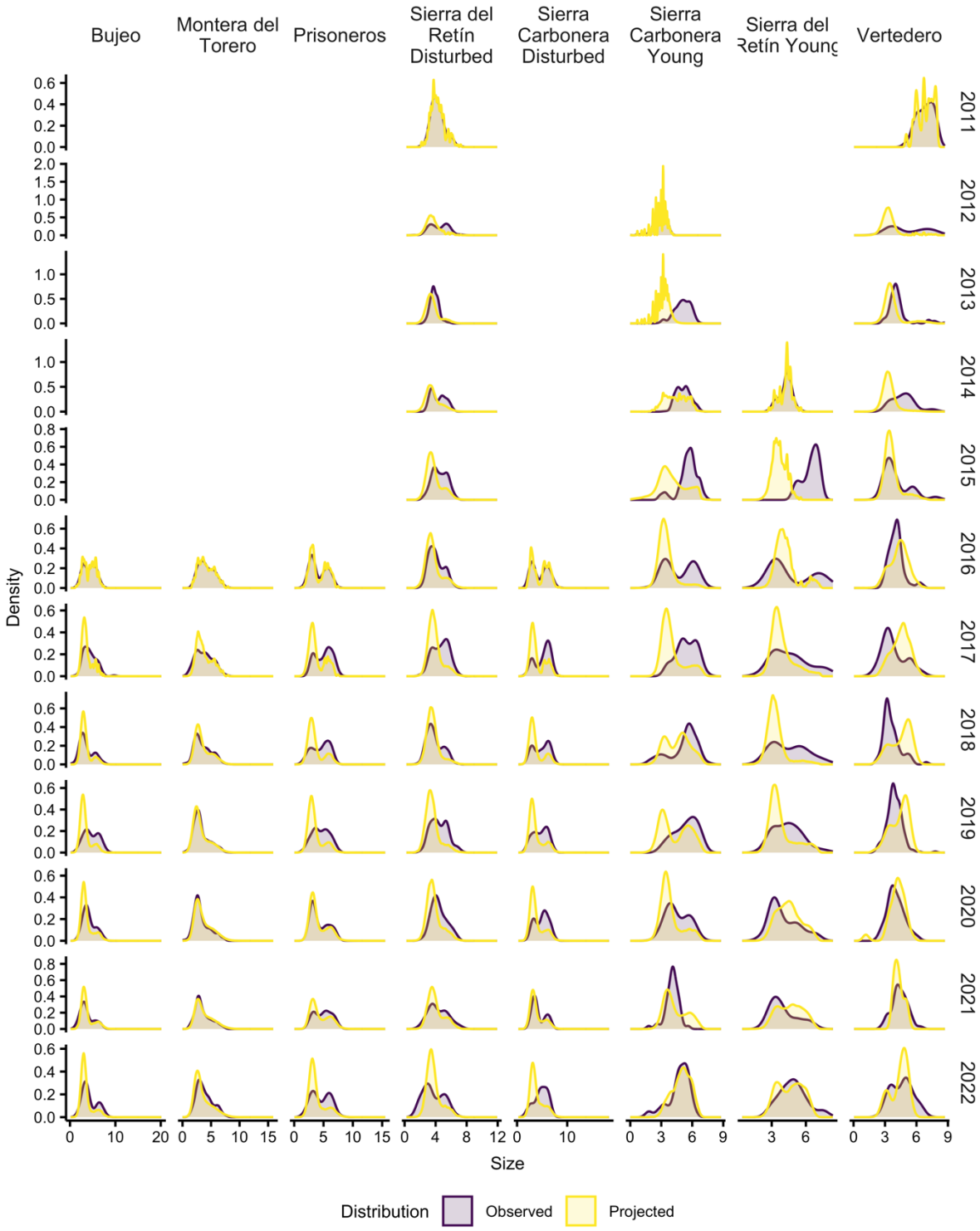


Figure S1 – Observed and projected aboveground population abundance. We projected each natural and anthropogenic population for 500 times across the range of observed years available for each population (maximum range from 2011 to 2022) to perform an out-of-sample validation of our individual-based model parameterization. For each projection, we obtained the average (line) and 25th and 95th (shaded ribbon) percentile of the aboveground population size. We compared these projected values to the observed ones (dots).



99 **Figure S2 – Observed and projected distributions of individual size across**
100 **time.** We projected each population from the first year it was sampled to 2022 and
101 obtained the site- and year-specific distributions of aboveground individual size, which
102 we compared to the observed distributions.
103

3. Covariate standardisation and correlation

We standardised all continuous covariates using the approach described by Gelman (2008):

$$\text{covariate}_{\text{scaled}(H)} = \frac{(\text{covariate}_{\text{unscaled}(H)} - \mu_{\text{covariate}_{\text{unscaled}(H)}})}{2 \cdot \sigma_{\text{covariate}_{\text{unscaled}(H)}}} \quad \text{(Equation 1)}$$

where μ and σ are respectively the mean and standard deviation of a given unscaled covariate in a subset of data from a given habitat *H* (natural or anthropogenic). In comparison with the common standardisation by one standard deviation, this standardisation approach enables the comparison of the effect sizes of both categorical (i.e. habitat) and continuous covariates (i.e. density-dependent variables).

We checked for correlations between covariates using the Pearson correlation coefficient (using the *cor* function from the stats R package; R Core Team, 2022). We considered a pair of variables to be correlated when the absolute value of the correlation coefficient was above 0.5. We included only one of the two correlated variables in a model, choosing the first to be retained in the model selection.

4. Vital-rate model selection

We assessed the nonlinear response of dewy-pine survival, growth, flowering probability, number of flowers, and seedling size to rainfall, maximum daily temperature, time since fire (TSF), aboveground density of large individuals (size >

129 4.5), and individual size using Generalised Additive Models (GAMs) fitted to
130 demographic data from individual dewy pines growing in natural or anthropogenic
131 habitats. We first assessed whether rainfall and temperature influenced vital rates
132 and in which period. We did this by comparing a null model (i.e., with only year and
133 population random effects, using a random effect basis (bs = “re”) in the mgcv
134 package; (Wood, 2017)) with models including cumulative rainfall or average
135 maximum daily temperature across different periods. As each census was done
136 during the flowering period, we assessed rainfall and temperature effect prior to the
137 annual population census for flowering probability, number of flowers, and seedling
138 size; or in the period between two annual censuses for survival and growth (see
139 Table S2 and Table S3). We considered further lagged climatic effects to be
140 captured by changes in plant size and density.

Table S2 – Periods of average maximum daily temperature and cumulative rainfall considered to assess the effect of temperature and rainfall on dewy-pine vital rates. We investigated the nonlinear response of dewy-pine vital rates to average maximum daily temperature (μ_{maxT}) and cumulative rainfall ($\sum_{rain}$) in various periods of the years prior (for flowering probability, number of flowers, and seedling size; in regular text) or post the annual population census (for survival and growth; in italic).

Period full name	Period short name	Period start	Period end
Previous winter average maximum daily temperature	$\mu_{maxT\_prevWinter}$	January	April
Previous fall cumulative rainfall	$\sum_{rain\_prevFall}$	September	November
Previous winter cumulative rainfall	$\sum_{rain\_prevWinter}$	January	April
Next summer average maximum daily temperature	$\mu_{maxT\_nextSummer}$	*May*	*September*
Next fall cumulative rainfall	$\sum_{rain\_nextFall}$	September	November
Next winter cumulative rainfall	$\sum_{rain\_nextWinter}$	January	April
Next fall and winter cumulative rainfall	$\sum_{rain\_nextFallWinter}$	September	April

We selected the best model among the possible rainfall and temperature periods using the Akaike Information Criterion (AIC), through the *model.sel* and *AICtab* functions of the MuMIn (Bartoń, 2022) and bbmle R packages (Bolker, 2022); we used a threshold of ΔAIC < 2 to identify models with no strong difference, and selected the model with the lowest number of degrees of freedom if more than one model were within that threshold. If both models with effects of rainfall and temperature performed better than the null model, we calculated Pearson's correlation coefficient using the *cor.test* function of the stats R package (R Core Team, 2022) to check whether the two variables were correlated. If they were (i.e., correlation coefficient > |0.5|), we used the AIC and the number of degrees of freedom to select the best model between the one with rainfall and the one with temperature. Conversely, if the two variables were not correlated (i.e., correlation coefficient ≤ |0.5|) We compared the models including one of rainfall and temperature to a model with both climatic variables, including their interaction (Table S3). Finally, we performed a forward selection—using the AIC and the degrees of freedom—, progressively adding aboveground density, size (except for seedling size), and time since fire (TSF; for natural populations only) in the model. While Table S3 only shows splines, we included the linear effects of all covariates in the model selection. We then included interactions between covariates in the model selection if at least one of them was retained in the single effect selection. Additionally, we included terms for site-specific random slopes (e.g., random size effect depending on the site).

Table S3 – Example of the model selection process. We selected the best model to predict a given vital rate (vr) using the Akaike Information Criterion (AIC). We first assessed whether rainfall and temperature affected the vital rate by comparing a null model (with only year and population random effects (**M1**) to models including rainfall or temperature values in various periods of the year (Step 1 for temperature and 2 for rainfall). If both models with temperature and rainfall performed better than the null model, we compared them with a model containing both climatic variables (Step 3), and also included their interaction (Step 4). We then progressively added size, time since fire (TSF), and aboveground density of large individuals (density) to see if their introgression improved the model (Steps 5–7). Finally, we included interactions between covariates when at least one of the two members of the interaction had been previously retained in the model selection (Steps 8–9). For each step, the *Best model according to the AIC* column shows the best model (**M**) according to the AIC. This model is then used as a comparison to the newer models in the next step. Newly added covariates at each time step are shown in green.

Model selection step	Models compared	Best model according to the AIC
1	**M1** = vr ~ s(time, bs = "re") + s(site, bs = "re") **M2** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re")	**M2**
2	**M3** = vr ~ s(time, bs = "re") + s(site, bs = "re") **M4** = vr ~ s(∑rain_prevFall, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M5** = vr ~ s(∑rain_prevFall, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re")	**M5**

3	**M2** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M5** = vr ~ s(∑rain_prevFall, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M6** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re")	**M6**
4	**M6** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M7** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re")	**M7**
5	**M7** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M8** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(size, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M9** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M10** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") +	**M9**

	s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re")	
6	**M9** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M11** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(size, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M12** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re")	**M12**

7	**M12** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M13** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + s(size, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re")	**M12**
8	**M12** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M14** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(μmaxT_prevWinter, density, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M15** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(μmaxT_prevWinter, TSF, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re")	**M15**

	M16 = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(μmaxT_prevWinter, size, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M17** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(∑rain_prevFall, density, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M18** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(∑rain_prevFall, TSF, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M19** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(∑rain_prevFall, size, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M20** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") +	

	ti(density, TSF, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M21** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(density, size, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M22** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(TSF, size, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re")	
9	**M15** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(μmaxT_prevWinter, TSF, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M23** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(μmaxT_prevWinter, TSF, k = 3, bs = "cr") + ti(μmaxT_prevWinter, density, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M24** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") +	**M15**

	ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(μmaxT_prevWinter, TSF, k = 3, bs = "cr") + ti(μmaxT_prevWinter, size, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M25** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(μmaxT_prevWinter, TSF, k = 3, bs = "cr") + ti(∑rain_prevFall, density, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M26** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(μmaxT_prevWinter, TSF, k = 3, bs = "cr") + ti(∑rain_prevFall, TSF, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M27** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(μmaxT_prevWinter, TSF, k = 3, bs = "cr") + ti(∑rain_prevFall, size, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M28** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") +	

	ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(μmaxT_prevWinter, TSF, k = 3, bs = "cr") + ti(density, TSF, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M29** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(μmaxT_prevWinter, TSF, k = 3, bs = "cr") + ti(density, size, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re") **M30** = vr ~ s(μmaxT_prevWinter, k = 3, bs = "cr") + s(∑rain_prevFall, k = 3, bs = "cr") + ti(μmaxT_prevWinter, ∑rain_prevFall, k = 3, bs = "cr") + s(density, k = 3, bs = "cr") + s(TSF, k = 3, bs = "cr") + ti(μmaxT_prevWinter, TSF, k = 3, bs = "cr") + ti(TSF, size, k = 3, bs = "cr") + s(time, bs = "re") + s(site, bs = "re")	

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5. Vital-rate estimation results

Table S4 – Most parsimonious generalised additive models for dewy-pine vital rates. For natural and anthropogenic populations, we estimated survival (σ), growth of aboveground plants (φ), flowering probability (p_{fl}), number of flowers ($n_{flowers}$), and seedling size (Φ) as a function of monthly average daily maximum temperature in a given period (μ_{maxT_period}), monthly cumulative rainfall in a given period ($\sum_{rain\_period}$), aboveground density of large individuals (density), individual size, and—for natural populations—time since fire (TSF). We selected the best model to predict a given vital rate using the Akaike Information Criterion (AIC). The function $s(x_{edf})$ is the spline smoothing function (i.e. simple effect) of x, and $ti(x, y_{edf})$ is the tensor product smoothing function of x and y. We used a cubic regression spline (bs = "cr" in the mgcv package; Wood, 2011; Wood et al., 2016; Wood, 2017) for all smoothing parameters, with a dimension k = 3 (except for the size effect on the number of flowers, where we used k = 4 to force a decline in the number of flowers of large individuals and avoid an ever-increasing number of flowers). Additionally, all models include a year and site random effect. edf is the corresponding effective degrees of freedom (Wood, 2017), which represents the amount of nonlinearity in the model component (edf = 1 corresponds to a linear fit), and n in the sample size. For the intercept and linear predictors (i.e., outside of s and ti smoothing functions), we report the estimated β-coefficients and the standard error.

Vital rate	Family (link function)	Most parsimonious model	*n*
Natural populations			
σ	Binomial (logit)	$-1.1_{(0.28)} + 0.27_{(0.47)}\mu_{maxT\_nextSummer} + 0.11_{(0.48)}\sum_{rain\_nextFall} + ti(\sum_{rain\_nextFall}, \mu_{maxT\_nextSummer}\ edf=0.88) + s(size\ edf=1.7) + s(TSF\ edf=0.00018) + s(\mu_{maxT\_nextSummer}, site\ edf=1.5, bs = "re") + ti(size, TSF\ edf=2.1) + ti(\sum_{rain\_nextFall}, density\ edf=2.7) - 1.4_{(0.46)}\sum_{rain\_nextFall}*TSF + ti(\mu_{maxT\_nextSummer}, size\ edf=0.74) - 0.26_{(0.096)}\mu_{maxT\_nextSummer}*density + ti(\mu_{maxT\_nextSummer}, TSF\ edf=0.93) + ti(\sum_{rain\_nextFall}, size\ edf=1.7) + s(time\ edf=3.8, bs = "re") + s(site\ edf=0.00010, bs = "re")$	1493
γ	Scaled *t* (identity)	$5.1_{(0.12)} + s(\sum_{rain\_nextFall}\ edf=0.000063) + 1.5_{(0.14)}size + s(TSF\ edf=1.7) - 0.074_{(0.018)}density + s(size, site\ edf=1.6, bs = "re") + ti(\sum_{rain\_nextFall}, TSF\ edf=0.81) + ti(\sum_{rain\_nextFall}, density\ edf=2.1) + ti(size, density\ edf=0.83) + s(time\ edf=0.000019, bs = "re") + s(site\ edf=1.8, bs = "re")$	482
p_{fl}	Binomial (logit)	$-4.0_{(0.57)} + 0.93_{(0.95)}\sum_{rain\_prevFall} + ti(\sum_{rain\_prevFall}, \mu_{maxT\_prevWinter}\ edf=1.5) + 5.5_{(0.44)}size + s(TSF\ edf=0.0000079) + ti(TSF, \mu_{maxT\_prevWinter}\ edf=0.91) + ti(TSF, density\ edf=0.58) + ti(\sum_{rain\_prevFall}, TSF\ edf=0.61) + ti(\sum_{rain\_prevFall}, density\ edf=1.3) + ti(size, density\ edf=1.2) + s(time\ edf=3.8, bs = "re") + s(site\ edf=0.000041, bs = "re")$	1487
$n_{flowers}$	Negative binomial (log)	$2.0_{(0.052)} + s(\mu_{maxT\_prevWinter}\ edf=0.00041) + s(size\ edf=2.8) - 0.40_{(1.4)}TSF + s(time\ edf=0.0013, bs = "re") + s(site\ edf=0.000056, bs = "re")$	185
Φ	Scaled *t* (identity)	$3.4_{(0.073)} + s(\mu_{maxT\_prevWinter}\ edf=0.66) + s(density\ edf=0.49) + 0.16_{(0.079)}TSF + s(density, site\ edf=0.000064, bs = "re") + s(TSF, site\ edf=0.69, bs = "re") + ti(\mu_{maxT\_prevWinter}, density\ edf=1.3) + ti(\mu_{maxT\_prevWinter}, TSF\ edf=0.76) + ti(density, TSF\ edf=0.69) + s(time\ edf=4.8, bs = "re") + s(site\ edf=0.000071, bs = "re")$	745
Anthropogenic populations			
σ	Binomial (logit)	$-0.55_{(0.60)} + s(\sum_{rain\_nextFall}\ edf=0.015) - 1.8_{(0.41)}\mu_{maxT\_nextSummer} + ti(\sum_{rain\_nextFall}, \mu_{maxT\_nextSummer}\ edf=0.00017) + s(size\ edf=1.9) + s(size, site\ edf=3.6, bs = "re") + s(\sum_{rain\_nextFall}, site\ edf=3.2, bs = "re") + ti(\sum_{rain\_nextFall}, size\ edf=0.92) + 0.11_{(0.037)}size*density + s(time\ edf=4.5, bs = "re") + s(site\ edf=3.9, bs = "re")$	6008
γ	Scaled *t* (identity)	$5.0_{(0.13)} + s(\mu_{maxT\_nextSummer}\ edf=0.37) + s(size\ edf=1.6) - 0.028_{(0.0053)}density + s(size, site\ edf=3.9, bs = "re") + s(\mu_{maxT\_nextSummer}, site\ edf=3.9, bs = "re") + s(time\ edf=3.9, bs = "re") + s(site\ edf=3.8, bs = "re")$	3202
p_{fl}	Binomial (logit)	$-4.7_{(0.36)} + s(\sum_{rain\_prevWinter}\ edf=0.50) + s(size\ edf=2.0) + s(density, edf=1.6) + s(size, site\ edf=3.6, bs = "re") + s(\sum_{rain\_prevWinter}, site\ edf=2.4, bs = "re") + s(density, site\ edf=2.7, bs = "re") + s(time\ edf=5.0, bs = "re") + s(site\ edf=3.0, bs = "re")$	6254
$n_{flowers}$	Negative binomial (log)	$1.9_{(0.072)} + s(\sum_{rain\_prevFall}\ edf=0.0012) + s(size\ edf=2.8) + s(\sum_{rain\_prevFall}, site\ edf=4.0, bs = "re") + s(size, site\ edf=3.7, bs = "re") + s(time\ edf=3.0, bs = "re") + s(site\ edf=0.015, bs = "re")$	899
Φ	Scaled *t* (identity)	$3.0_{(0.14)} + s(\mu_{maxT\_prevWinter}\ edf=0.50) - 0.057_{(0.012)}density + s(\mu_{maxT\_prevWinter}, site\ edf=2.9, bs = "re") + s(density, site\ edf=1.9, bs = "re") + ti(\mu_{maxT\_prevWinter}, density\ edf=0.64) + s(time\ edf=5.5, bs = "re") + s(site\ edf=3.9, bs = "re")$	2608

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Among-site variation in average vital rates and climate effects

Dewy-pine vital rates varied between natural and anthropogenic habitat as well as between sites. Among-site variation was larger in anthropogenic than in natural conditions, possibly because of the among-population differences in the level of anthropogenic disturbance. This variation was especially large for survival rates, which ranged from 0.11 [0.058, 0.20] in Bujeo to 0.80 [0.72, 0.86] in Montera del Torero, while it remained stable at 0.27 [0.17, 0.40] on average in natural populations (Fig. S3).

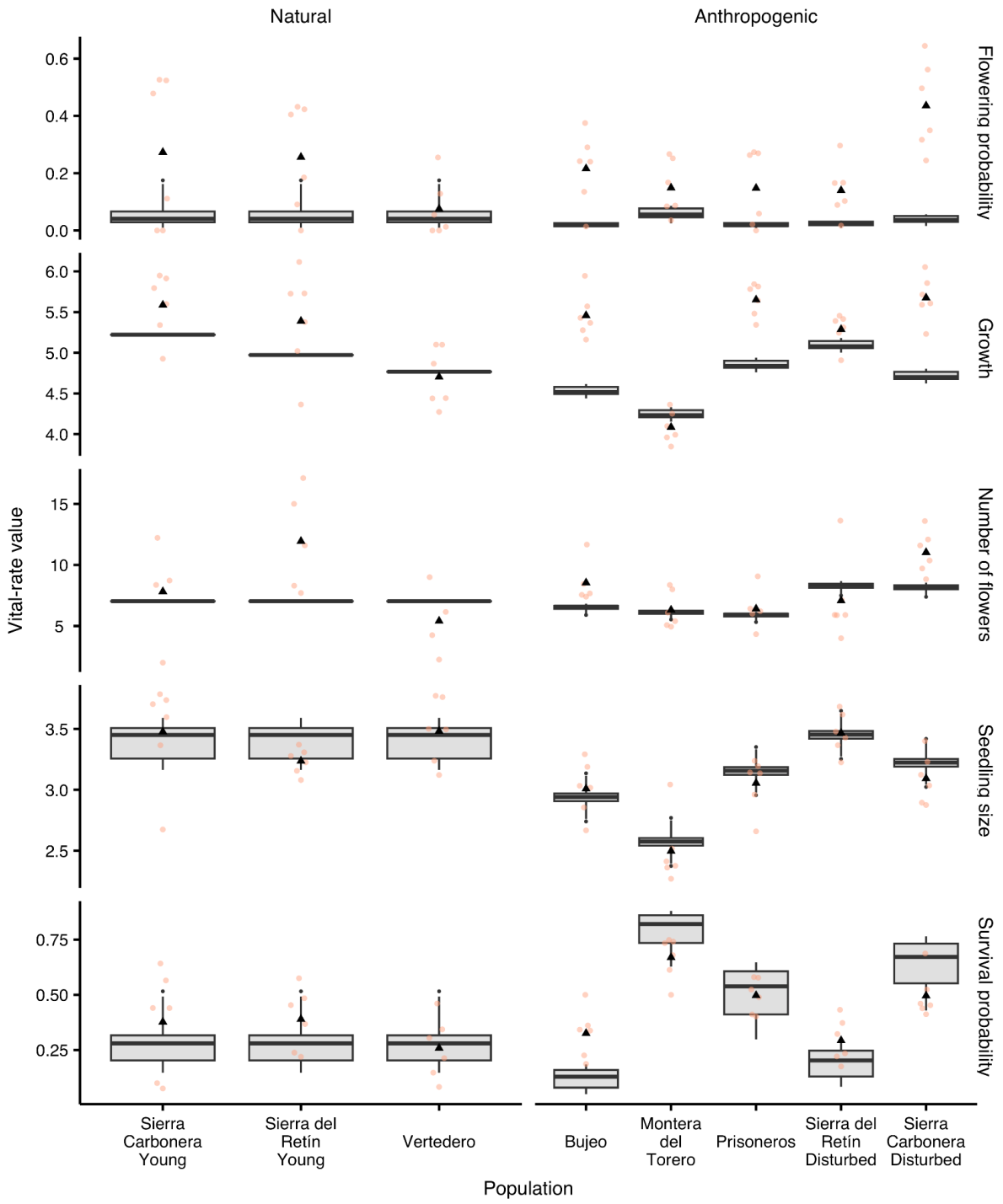

Figure S3 – Among-site variation in average vital-rate values in natural and anthropogenic populations. The boxplots represent the distribution of the average values of site-specific survival, growth, and flowering rates, as well as the number of flowers and seedling size estimated for each year. The 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.

In anthropogenic habitats, we found among-site disparities in the direction of association between climatic variables and survival, growth, number of flowers per individual, and seedling size (Fig. S4). For instance, the number of flowers was positively associated with increasing rainfall in Montera del Torero population (e.g. from 5.5 [5.0, 6.1] under 100 mm of rain to 7.0 [6.3, 7.8] under 200 mm), but negatively in Sierra del Retín Disturbed (e.g. from 8.7 [7.5, 9.9] to 7.3 [6.4, 8.4]). In contrast, there was no such among-site variation in natural habitats. For example, seedlings were bigger with higher winter temperatures (January–April); seedling size increased from 3.0 [2.8, 3.3] under 16 °C to 3.4 [3.3, 3.6] under 18 °C (Fig. S5).

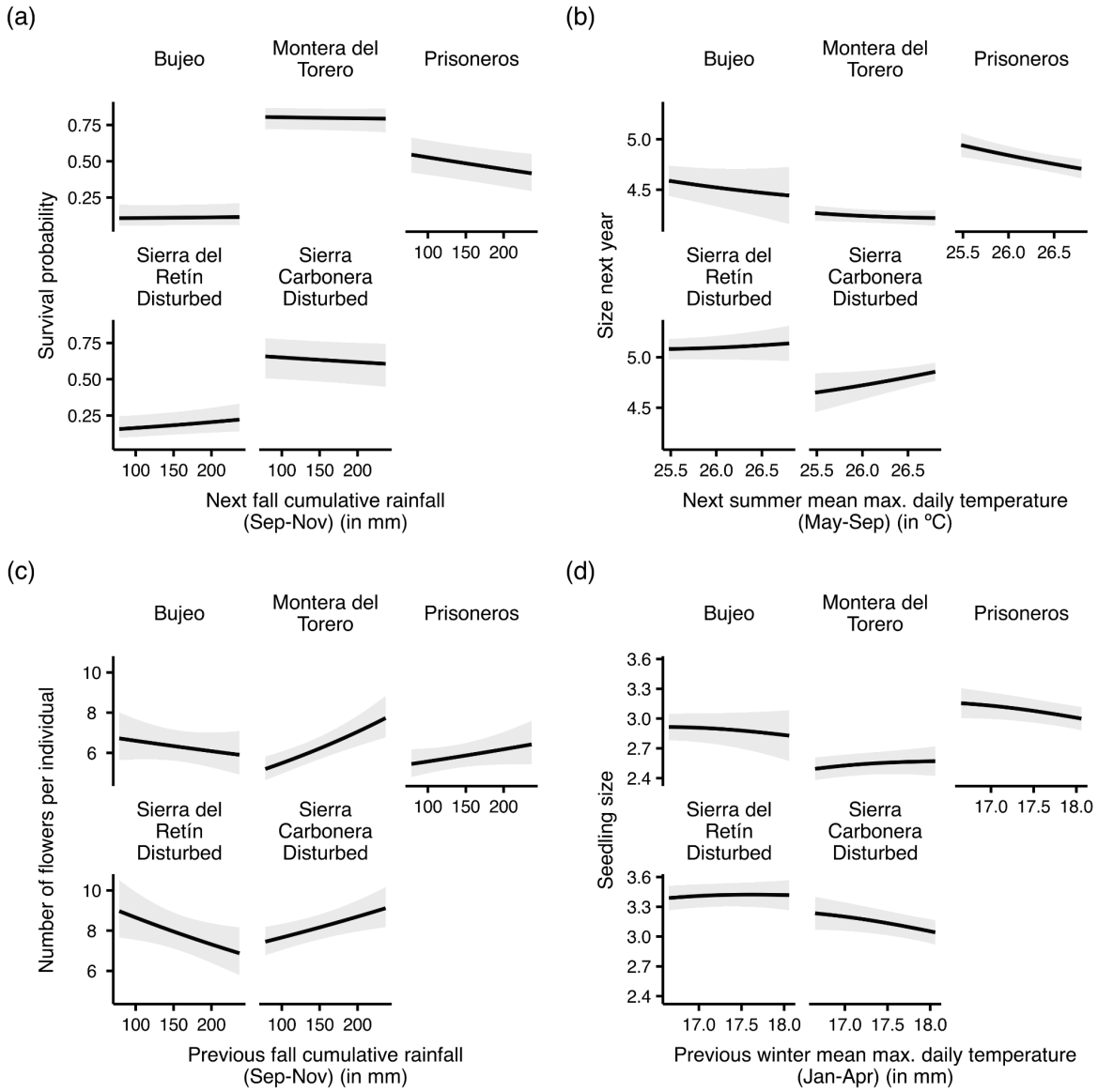

Figure S4 – Among-site variation in the association between climatic variables and vital rates in anthropogenic populations. We predicted the values of (a) survival probability, (b) size in the next year, (c) number of flowers per individual, and (d) seedling size for a range of rainfall and temperature values in each anthropogenic population of dewy pines. The lines represent the average vital-rate value and the shaded ribbon the 95% confidence interval. We kept all other

covariates at their mean values (scaled value = 0) except for the number of flowers, where we used the mean size of reproducing individuals.

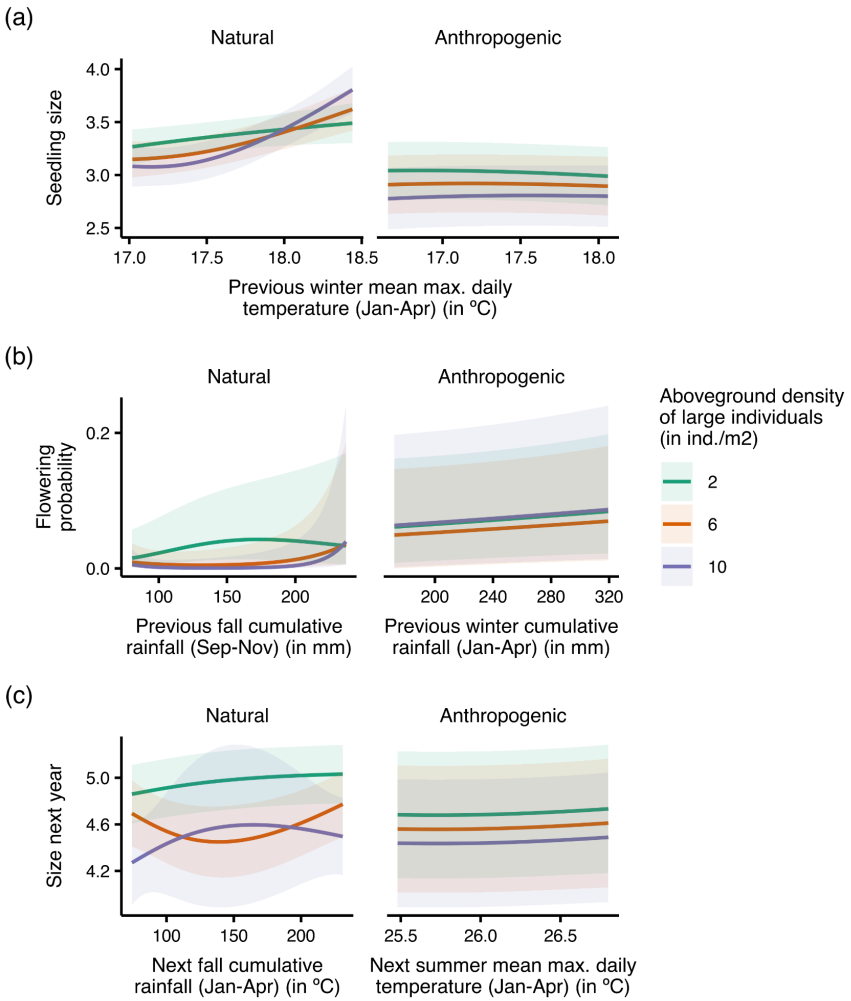

Figure S5 – Density-dependent variation in vital-rate responses to climate. We predicted the values of (a) seedling size, (b) flowering probability, and (c) size in the next year for a range of rainfall and temperature values and three levels of aboveground densities in natural and anthropogenic habitats. The lines represent the average vital-rate value and the shaded ribbon the 95% confidence interval. We kept all other covariates at their mean values (scaled value = 0) except for the number of flowers, where we used the mean size of reproducing individuals.

Vital-rate responses to large aboveground individual density and climate-density interactions

Seedling size decreased with higher numbers of large individuals aboveground (from 3.0 [2.8, 3.3] at 2 ind./m^2 to 2.8 [2.5, 3.1] at 10 ind./m^2 in anthropogenic populations and from 3.4 [3.2, 3.5] to 3.1 [3.0, 3.3] in natural ones; Fig. S5a; Table S5). Density also mediated the association between seedling size and winter temperature in natural populations, with a stronger positive correlation between the two variables with 6 ind./m2 (3.2 [3.1, 3.4] at 17.5 ºC and 3.7 [3.4, 3.9] at 18.5 ºC) than with 2 ind./m2 (3.4 [3.2, 3.5] and 3.5 [3.3, 3.7]) (Fig. S5a; Table S5). Additionally, with high densities in natural populations, flowering probability was low except for high amounts of rainfall (e.g. with 6 ind./m2, 0.19 [0.035, 0.60] for 150 mm of rainfall and 0.37 [0.096, 0.76] for 200 mm; but with 2 ind./m2, 0.71 [0.43, 0.88] and 0.71 [0.38, 0.90]) (Fig. S5b; Table S5), and the pattern was similar for growth (e.g. with 6 ind./m2, 4.5 [4.1, 4.8] for 150 mm of rainfall and 4.6 [4.3, 4.9] for 200 mm; but with 2 ind./m2, 5.0 [4.7, 5.2] and 5.0 [4.8, 5.3]) (Fig. S5c; Table S5).

Vital-rate responses to time since fire and size

As expected from previous work and observations, individuals in natural populations had a short lifespan, as indicated by the decrease in survival with time since fire (TSF) (0.42 [0.28, 0.57] and 0.29 [0.18, 0.42] respectively 3 and 7 years after a fire) and size (0.26 [0.16, 0.40] with a size of 5.0 and 0.22 [0.12, 0.37] with 6.2) (Fig. S6a,b; Table S5). This early decline in survival was accompanied by investment into reproduction from early post-fire stages, with flowering probability decreasing from

0.16 [0.038, 0.48] to 0.051 [0.016, 0.15] respectively 3 and 7 years after a fire and the number of flowers per individual from 10 [8.2, 13] to 7.6 [6.8, 8.4] (Fig. 5c,d; Table S5). Dewy pines growing in natural conditions also appeared to reproduce throughout most of their lifetime, as both flowering probabilities and number of flowers continuously increased with size (individuals had a probability of flowering of 0.17 [0.061, 0.38] and 2.9 [2.4, 3.5] flowers with a size of 5.0, which respectively increased to 0.74 [0.47, 0.90] and 7.8 [6.9, 8.7] with 6.2) (Fig. S6e,f; Table S5). In contrast, the largest individuals had the highest survival in anthropogenic habitats (0.61 [0.32, 0.84] and 0.75 [0.46, 0.91] with sizes of 5.0 and 6.2; Fig. S6b; Table S5), but did not invest as much in reproduction with both flowering probability and number of flowers declining after reaching a peak for a size of 7.3 (probability of flowering of 0.69 [0.34, 0.91]) and 8.2 (19 [13, 28] flowers) (Fig. S6e,f; Table S5).

Vital-rate responses to size-climate interactions

In natural populations, small individuals survived best at intermediate rainfall (e.g. 0.29 [0.18, 0.43] with 150 mm of rain for an individual of size 3.4) than for high or low amounts of rainfall (0.18 [0.098, 0.30] with 80 mm and 0.26 [0.14, 0.43] with 210 mm), while large individuals survived best at low or high rainfall (e.g., for an individual of size 6.6, 0.26 [0.13, 0.45] with 80 mm, 0.20 [0.10, 0.37] with 150 mm, and 0.26 [0.13, 0.45] with 210 mm; Fig. S6g; Table S5). Additionally, survival rates decreased faster with summer temperature for large than for small individuals (from 0.60 [0.32, 0.83] at 25 °C to 0.26 [0.13, 0.44] at 26 ºC with a size of 6.6, and from 0.57 [0.32, 0.79] to 0.34 [0.22, 0.49] with a size of 3.4; Fig. S6h; Table S5). We also found size dependence in the association between survival and rainfall in

anthropogenic populations, where large individuals survived best at intermediate amounts of rain in fall (e.g., for an individual with a size of 6.6, 0.67 [0.37, 0.88] at 80 mm of rain, 0.78 [0.49, 0.93] at 150 mm, and 0.73 [0.44, 0.91] at 210 mm), while small individuals were not affected by changes in rainfall (Fig. S6g; Table S5).

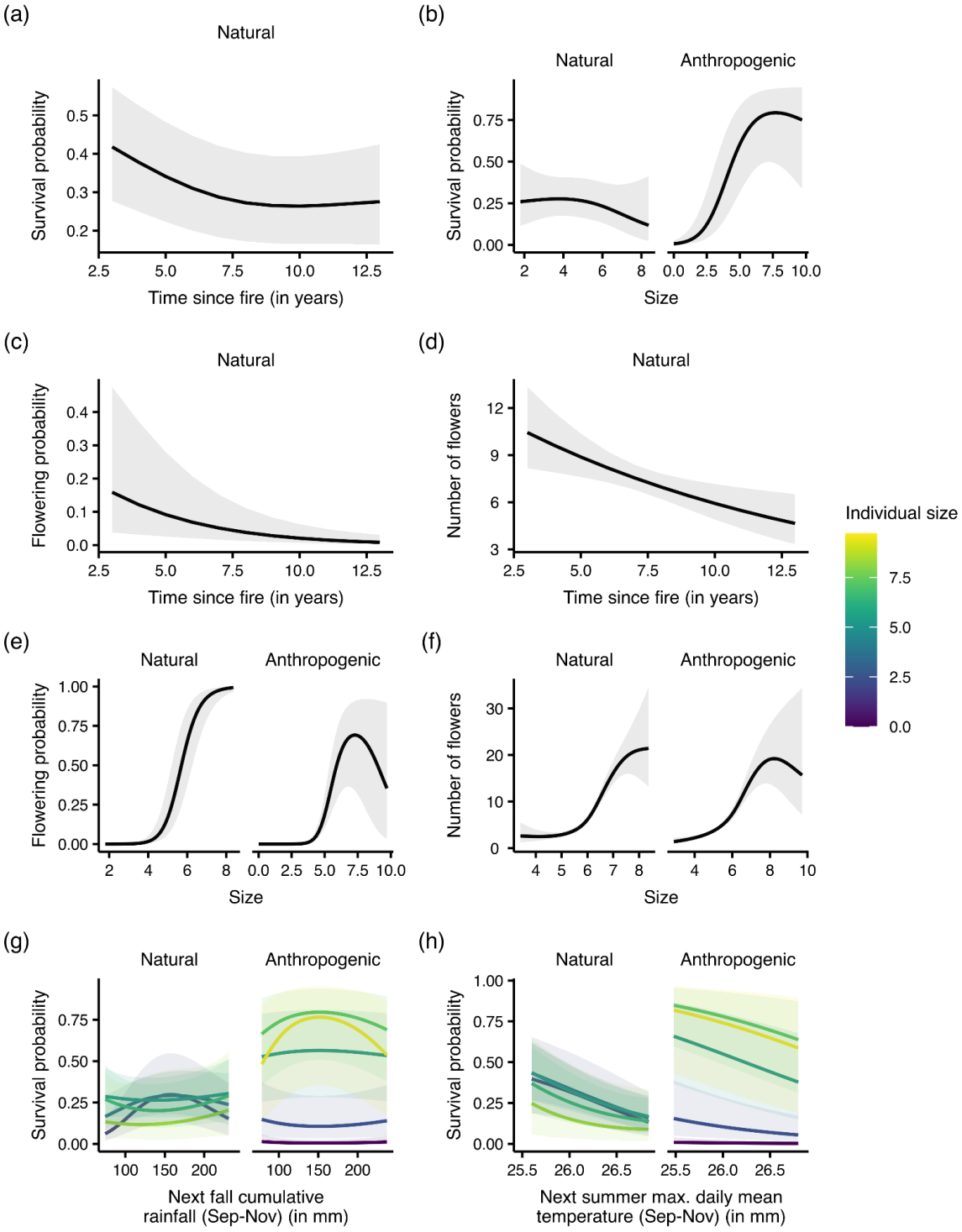

Figure S6 – Vital-rate responses to time since fire, size, and size-climate interactions. We predicted the values of survival and flowering probability as well as the number of flowers per individual for a range of number of years since the last fire (time since fire) in natural habitats (a, c, d) and for a range of individual sizes in both natural and anthropogenic habitats (b, e, f). Finally, we predicted the values of survival probability for a range of individual sizes as well as (h) rainfall and (g) temperature values. The lines represent the average vital-rate value and the shaded ribbon the 95% confidence interval. In each case, we kept all other covariates at their mean values (scaled value = 0) except for the number of flowers, where we used the mean size of reproducing individuals.

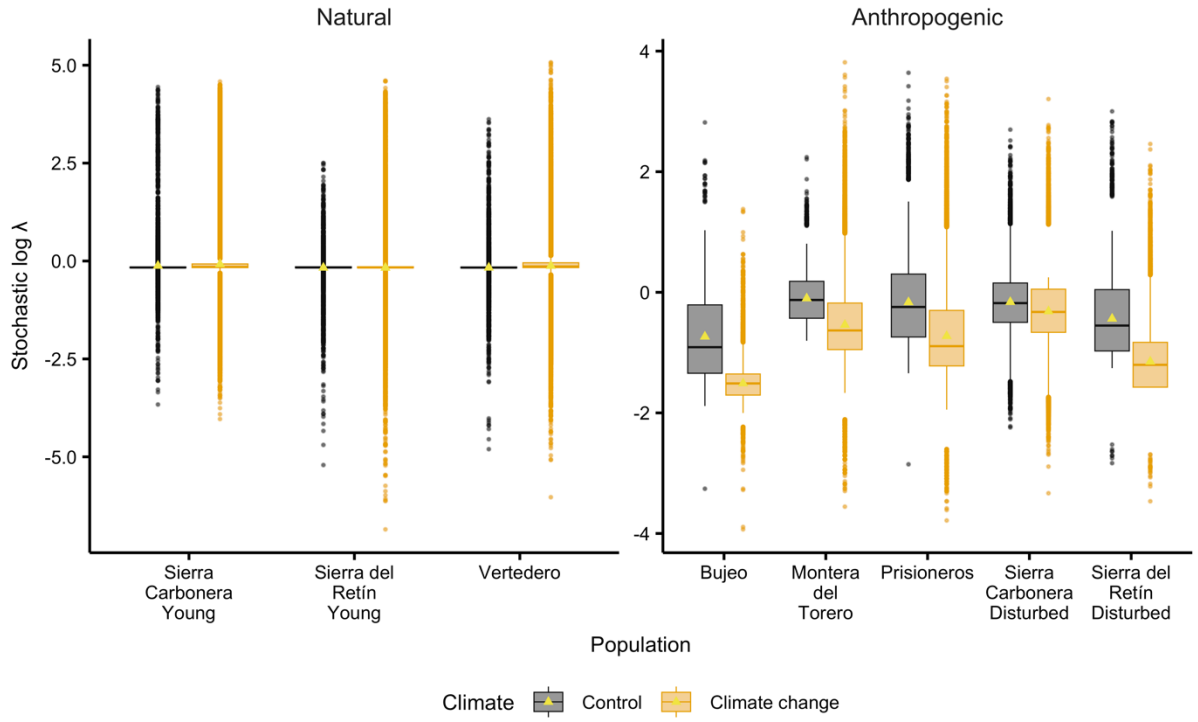

Figure S7 – Site-specific population growth rate. For each population, we calculated the stochastic growth rate log λ_S as the average of all annual log λ in each of 500 projections.

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

1. Current rainfall and temperature data

We modelled the response of dewy-pine vital rates to rainfall and maximum daily temperature using observed daily climatic data at dewy-pine population locations (Table 1) from the E-OBS dataset from the EU-FP6 project UERRA and the Copernicus Climate Change Service (Cornes et al., 2018; accessible at https://surfobs.climate.copernicus.eu/dataaccess/access_eobs.php). We used the ncdf4 R package to process the raw netCDF weather data (Pierce, 2021), and transformed the daily rainfall and maximum daily temperature into monthly cumulative rainfall and average maximum daily temperature. For each population, we then obtained monthly cumulative rainfall and average maximum temperature data from the year prior the first census (i.e., 2010 for Sierra del Retín Disturbed and Vertedero, 2011 for Sierra Carbonera Young, 2014 for Sierra del Retín Young, and 2015 for all other populations). To do so, we averaged the recorded climate values within a buffer of 0.1×1.5 degrees around the GPS location of each population.

Table S1 – GPS locations of dewy-pine populations. Longitude and latitude of population locations are given in decimal degrees.

Population	Habitat type	Latitude	Longitude	First sampled	Last fire
Sierra Carbonera Young	Natural	36.209722 or 36°13' N	-5.36 or 5°22' W	2012	2011
Sierra del Retín Young	Natural	36.17694444 or 36°11' N	-5.833055556 or 5°50' W	2015	2013
Vertedero	Natural	36.121667 or 36°7' N	-5.49 or 5°29' W	2011	2009
Sierra del Retín Disturbed	Anthropogenic	36.198056 or 36°12' N	-5.823611 or 5°49' W	2011	1996
Prisioneros	Anthropogenic	36.105 or 36°6' N	-5.486388889 or 5°29' W	2016	1950
Bujeo	Anthropogenic	36.072461 or 36°4' N	-5.52654 or 5°32' W	2016	1950
Montera del Torero	Anthropogenic	36.226389 or 36°14' N	-5.585278 or 5°35' W	2016	1950
Sierra Carbonera Disturbed	Anthropogenic	36.10638889 or 36°12' N	-5.360555556 or 5°22' W	2016	1950

2. Projected rainfall and temperature data

To project dewy-pine populations under climate change, we used projected rainfall and temperature values at dewy-pine population locations from 11 global circulation models (GCM; see Table 2) 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 (ESFG; Petrie et al., 2021; available at https://aims2.llnl.gov/search). For each model, we selected the best variant using the GCMeval tool (Parding et al., 2020; accessible at

https://gcmeval.met.no/). For each GCM, we downloaded data for the worst scenario of atmospheric greenhouse gas Representative Concentration Pathway (RCP), corresponding to a level of radiative forcing reaching 8.5 Watts per square metre (Wm^{-2}) by 2100 (RCP 8.5). We processed the raw data from each climate projection model using the ncdf4 R package (Pierce, 2021) to obtain monthly cumulative rainfall and average maximum temperature in each population by averaging the values recorded within a buffer of 0.1×1.5 degrees around the population coordinates (i.e., 1.5 times the grid resolution).

Most GCMs comprised projected rainfall and temperature values beyond the values observed in our populations. To avoid predicting vital rates using values of climate variables outside the observed range, we capped these values to the maximum and minimum observed. For example, while the observed maximum cumulative rainfall in fall was 245 mm, six of the considered GCM predicted greater values in some years, ranging from 250 to 463 mm; we transformed these values to the maximum observed (245 mm). This allowed us to investigate the response of dewy-pine populations to increases in the frequency of extreme climatic conditions, rather than changes in absolute rainfall and temperature values.

Table S2 – List of global circulation models used to project dewy-pine populations under climate change.

Source ID	Experiment	Variant	Version	Institution	Modelling centre	Citation
CanESM5	ssp585	r1i1p1f1	20190429	Canadian Centre for Climate Modelling and Analysis, Environment and Climate Change Canada, Victoria, BC V8P 5C2, Canada	CCCma	(Swart et al., 2019)
EC_Earth3	ssp585	r4i1p1f1	20200425	AEMET, Spain; BSC, Spain; CNR-ISAC, Italy; DMI, Denmark; ENEA, Italy; FMI, Finland; Geomar, Germany; ICHEC, Ireland; ICTP, Italy; IDL, Portugal; IMAU, The Netherlands; IPMA, Portugal; KIT, Karlsruhe, Germany; KNMI, The Netherlands; Lund University, Sweden; Met Eireann, Ireland; NLeSC, The Netherlands; NTNU, Norway; Oxford University, UK; surfSARA, The Netherlands; SMHI, Sweden; Stockholm University, Sweden; Unite ASTR, Belgium; University College Dublin, Ireland; University of Bergen, Norway; University of Copenhagen, Denmark; University of Helsinki, Finland; University of Santiago de Compostela, Spain; Uppsala University, Sweden; Utrecht University, The Netherlands; Vrije Universiteit Amsterdam, the Netherlands;	EC-Earth-Consortium	(EC-Earth Consortium (EC-Earth), 2019)

				Wageningen University, The Netherlands. Mailing address: EC-Earth consortium, Rossby Center, Swedish Meteorological and Hydrological Institute/SMHI, SE-601 76 Norrkoping, Sweden		
FGOALS_G3	ssp585	r1i1p1f1	20190818	Chinese Academy of Sciences, Beijing 100029, China	CAS	(Li, 2019)
GFDL_ESM4	ssp585	r1i1p1f1	20180701	National Oceanic and Atmospheric Administration, Geophysical Fluid Dynamics Laboratory, Princeton, NJ 08540, USA	NOAA-GFDL	(John et al., 2018)
GISS_E2_1_G	ssp585	r1i1p1f2	20200115	Goddard Institute for Space Studies, New York, NY 10025, USA	NASA-GISS	(NASA Goddard Institute for Space Studies (NASA/GISS), 2020)
INM_CM4_8	ssp585	r1i1p1f1	20190603	Institute for Numerical Mathematics, Russian Academy of Science, Moscow 119991, Russia	INM	(Volodin et al., 2019)
IPSL_CM6A_LR	ssp585	r1i1p1f1	20190903	Institut Pierre Simon Laplace, Paris 75252, France	IPSL	(Boucher et al., 2019)
MIROC6	ssp585	r1i1p1f1	20191016	JAMSTEC (Japan Agency for Marine-Earth Science and Technology, Kanagawa 236-0001, Japan), AORI (Atmosphere and Ocean Research Institute, The University of Tokyo, Chiba 277-8564, Japan), NIES (National Institute for Environmental Studies, Ibaraki 305-8506, Japan), and R-	MIROC	(Shiogama et al., 2019)

				CCS (RIKEN Center for Computational Science, Hyogo 650-0047, Japan)		
MPI_ESM1_2_LR	ssp585	r10i1p1f1	20190710	Max Planck Institute for Meteorology, Hamburg 20146, Germany	MPI-M	(Wieners et al., 2019)
MRI_ESM2_0	ssp585	r1i1p1f1	20191108	Meteorological Research Institute, Tsukuba, Ibaraki 305-0052, Japan	MRI	(Yukimoto et al., 2019)
NorESM2_MM	ssp585	r1i1p1f1	20191108	NorESM Climate modeling Consortium consisting of CICERO (Center for International Climate and Environmental Research, Oslo 0349), MET-Norway (Norwegian Meteorological Institute, Oslo 0313), NERSC (Nansen Environmental and Remote Sensing Center, Bergen 5006), NILU (Norwegian Institute for Air Research, Kjeller 2027), UiB (University of Bergen, Bergen 5007), UiO (University of Oslo, Oslo 0313) and UNI (Uni Research, Bergen 5008), Norway. Mailing address: NCC, c/o MET-Norway, Henrik Mohns plass 1, Oslo 0313, Norway	NCC	(Bentsen et al. 2019)

3. Current and future climatic trends

Temperatures have increased in the past decades, with an average trend (mean and 95% confidence interval) of 0.033 ºC [0.021; 0.044] per year between

1980 and 2022. This trend will continue and intensify in the future, as climate-change models predict an increase of 0.055 ºC [0.053; 0.057] per year on average between 2015 and 2100 under the RCP 8.5 global change scenario (Moss et al., 2010; van Vuuren et al., 2011; Riahi et al., 2011). Average monthly cumulative rainfall and its variability show opposite trends between the current and projected conditions. Both the yearly mean and variability increased on average between 1980 and 2022 (0.18 [-0.23, 0.59] and 0.083 mm [-0.47, 0.63] per year, respectively) but are predicted to decrease until 2100 according to future projections under the RCP 8.5 scenario (-0.16 [-0.19, -0.13] and -0.11 mm [-0.14, -0.077]). Notably, while the RCP 4.5 global change scenario predicts a more moderate increase in temperature, both scenarios show the same trend for the 30 years of our projections (Fig. S1; Fig. S2a).

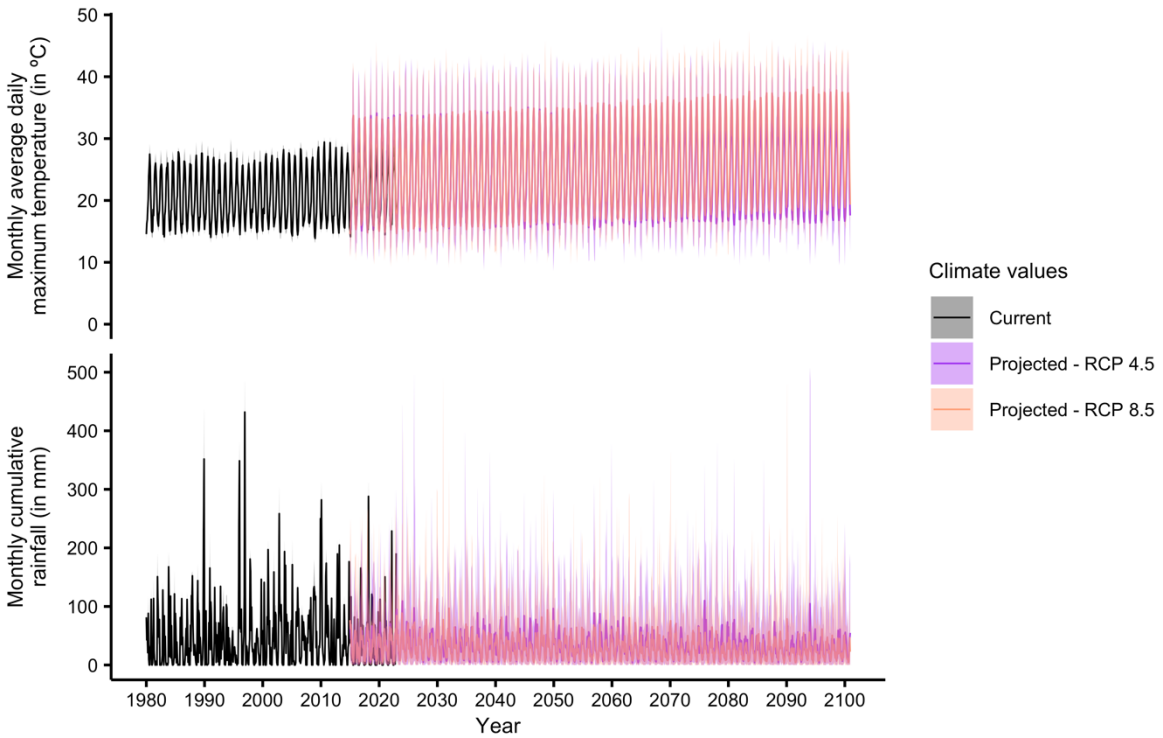

Figure S1 – Current and projected monthly temperature and rainfall data.

We obtained current data on daily maximum temperature and daily rainfall amounts from the E-OBS dataset from the EU-FP6 project UERRA and the Copernicus Climate Change Service. We extracted the projected rainfall and temperature values

under the RCP 4.5 and 8.5 global change scenarios from 11 global change models from the Coupled Model Intercomparison Project 6 (CMIP6; available from the Earth System Grid Federation).

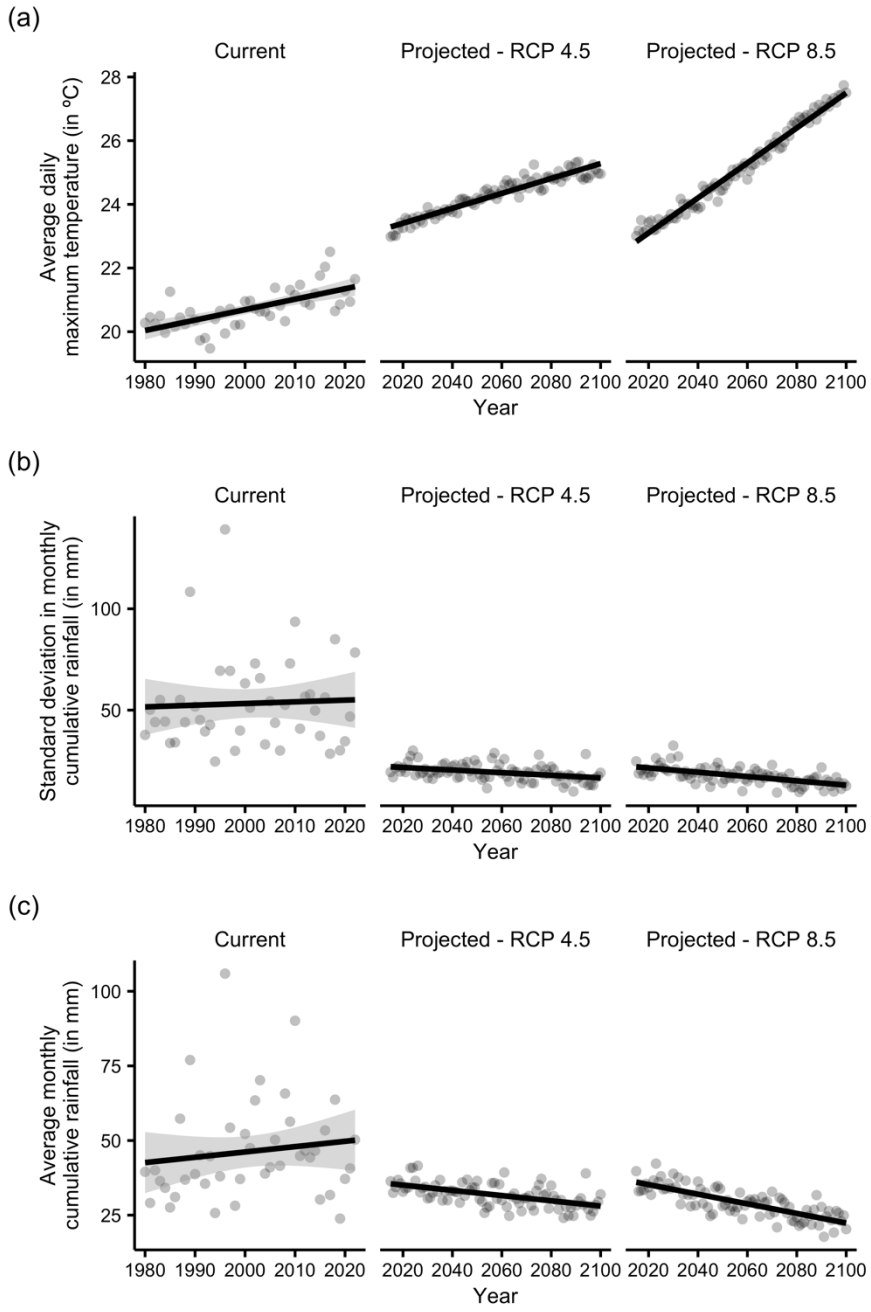

Figure S2 – Current and projected trends in temperature and rainfall. We investigated yearly changes in (a) average daily maximum temperature, (b) standard deviation in monthly cumulative rainfall, and (c) average monthly cumulative rainfall, for the current (1980–2022) and projected conditions (2015–2100) under the RCP

4.5 and 8.5 global change scenarios. Dots represent the observed values and lines and shaded ribbons represent the mean and 95% confidence interval of linear models fitted to each data subset.

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Appendix S3 – Individual-based model description

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al., 2006), as updated by (Grimm et al., 2020).

1. Purpose and patterns

The purpose of the model is to predict population growth rates and extinction probabilities of dewy-pine (*Drosophyllum lusitanicum*) populations in natural and anthropogenic habitats in response to projected changes in rainfall and temperature values. We evaluate our model by its ability to reproduce the observed dynamics in the mean changes in aboveground abundance in each population, or at least follow a similar trend.

2. Entities, state variables, and scales

Entities and state variables

The **environment** is a single entity representing the population. Its role is to describe the environment (e.g. climate variables) and keep track of simulated time. Environment state variables correspond to dynamic global variables and are presented in Table 1.

Table 1 – Environment state variables

Variable name	Variable type and units	Range	Meaning
time_sim	Integer; dynamic	≥1	Number of years that passed since the start of the projection
year_obs	Integer; dynamic (e.g. 2020)	≥2016	Current year in the projection
year	Integer; dynamic (e.g. 2020)	≥2016	Year randomly sampled from the available observed years
TSF	Integer; dynamic	≥0	Number of years since the last fire
TSFcat	Categorical; dynamic (0–4)	{0, 1, 2, 3, 4}	Post-fire habitat stage, with any number of years after a fire ≥ 4 corresponding to 4
corr_seed_surv	Probability; dynamic	[0, 1]	Correction factor representing the survival probability of seeds above the ground
summerT	Real number; °C; dynamic	≥0	Average minimum daily temperature in summer (May–September) following the annual survey in May
prevwinterT	Real number; °C; dynamic	≥0	Average minimum daily temperature in winter (January–April) prior to the annual survey in May
fallR	Integer; mm; dynamic	≥0	Cumulative rainfall in fall (September–November) following the annual survey in May
prevfallR	Integer; mm; dynamic	≥0	Cumulative rainfall in fall (September–November) prior to the annual survey in May
prevwinterR	Integer; mm; dynamic	≥0	Cumulative rainfall in winter (January–April) prior to the annual survey in May
extinction	Binary; dynamic	{0, 1}	Current state of the population: extinct (1) or not (0)

Plants are entities representing the aboveground—as opposed to seeds—individual dewy pines in the population. They correspond to individuals from the seedling stage

in the species life cycle. The state variables unique to each plant are presented in Table 2.

Table 2 – Plant state variables

Variable name	Variable type and units	Range	Meaning
ID	Character string; static	NA	Unique identifier of the plant
quadratID	Character string; static	NA	Unique identifier of the quadrat corresponding to the location of the plant
size	Real number; dynamic	≥0	Plant size in the current time step, corresponding to log(number of leaves x length of the longest leaf in cm)
survival	Binary; dynamic	{0, 1}	State of the plant at the next time step: alive (1) or dead (0)
sizeNext	Real number; dynamic	≥0	Plant size in the next time step, corresponding to log(number of leaves x length of the longest leaf in cm)
flowering	Binary; dynamic	{0, 1}	Reproductive state of the plant in the current time step: flowering (1) or not (0)
nbFlowers	Integer; dynamic	≥0	Number of flowers on the plant
nb_seeds	Integer; dynamic	≥0	Number of seeds per flower produced by the plant

Seeds are entities representing individuals before they germinate and become seedlings. Because they are concerned by different processes, we divided seeds between two types of entities: **Seedbank seeds** are entities representing the seeds in the soil seedbank and **produced seeds** are entities representing the individuals that have been produced by aboveground reproducing dewy pines in the current time step. Their state variables are presented in Table 3 and Table 4.

39 **Table 3 – Seedbank seed state variables**

Variable name	Variable type and units	Range	Meaning
ID	Character string; static	NA	Unique identifier of the seed
quadratID	Character string; static	NA	ID of the quadrat corresponding to the location of the seed
size	Real number; dynamic	≥0	Size of the seedling growing from the germinating seed in the next time step, corresponding to log(number of leaves x length of the longest leaf in cm)
outSB	Binary; dynamic	{0, 1}	Seed germination (1) or not (0)
staySB	Binary; dynamic	{0, 1}	Seed dormancy (1) or not (0)

40

41 **Table 4 – Produced seed state variables**

Variable name	Variable type and units	Range	Meaning
ID	Character string; static	NA	Unique identifier of the seed
quadratID	Character string; static	NA	ID of the quadrat corresponding to the location of the seed
size	Real number; dynamic	≥0	Size of the seedling growing from the germinating seed in the next time step, corresponding to log(number of leaves x length of the longest leaf in cm)
goCont	Binary; dynamic	{0, 1}	Seed germination (1) or not (0)
goSB	Binary; dynamic	{0, 1}	Seed entering the seedbank (1) or not (0)

42

Quadrats are two-dimensional squares representing the monitoring units in which plants are censored in a population. Quadrats are only associated with one dynamic state variable, *abLarge*, an integer (≥0) corresponding to the number of plants with a size > 4.5 present in a quadrat.

Scales

The model is spatially explicit and represents a population in a two-dimensional space extending over 40 m^2 divided in 1-m^2 quadrats. These quadrats are discrete units in which individual plants and seeds are distributed, and correspond to the units in which dewy pines are monitored every year—more specifically in four separated transects of ten quadrats each.

The model represents time via discrete time steps, each corresponding to one year, to replicate the annual surveys that take place in May in the various populations.

3. Process overview and scheduling

Process overview

The model covers the life cycle of dewy pines. At each time step, the **environment** updates the environmental variables and simulation time; the **plants** reproduce, survive, and grow; the **seedbank seeds** germinate or stay dormant; and the **produced seeds** germinate or go to the seedbank. The **quadrats** get new aboveground density values.

Schedule summary

Throughout the model, the update of each state variable through a given process for **plants** and **produced** or **seedbank seeds** is done simultaneously for all entities, as each process in a given entity is assumed to be independent from the processes in another entity.

At each timestep, the model resets the ensemble of **seeds produced** to zero. The population of **plants** is also reset if a fire occurred, as all aboveground individuals are burned. The **environment** then updates the environmental variables (rainfall and temperature) as well as the simulation year and the number of years after the last fire. The latter two are used to update the correction factor representing seed survival (*corr_seed_surv*).

Aboveground **plants** then reproduce (see *Reproduction* submodel); that is, they flower and produce a certain number of flowers, which in turn produce seeds. The number of flowers is capped to the user-selected value if needed. The fate of the **seeds produced** is updated; they can either germinate, contribute to the seedbank, or die (i.e., none of the two former processes). **Produced seeds** that do not die are then assigned an ID, and those that germinate a size, and the maximum ID number is updated.

After reproducing, **plants** survive and grow (*Survival and growth* submodel). The size is capped or adjusted if needed. Seedbank processes take place next (*Seedbank* submodel), with **seedbank seeds** germinating, staying dormant, or dying

(i.e., none of the two former processes). Seeds that germinate are attributed a size. **Produced seeds** that were assigned to go dormant are added to the seedbank, and those that germinate are added to the aboveground population after capping their number in each **quadrat**.

After each timestep, the population growth rate and mean change in aboveground population abundance are calculated and the yearly individual data is merged to the full data. The **environment** updates the simulation time and the extinction status to 1 if the quasi-extinction threshold is reached, and the size of each surviving **plant** is updated to its size at the next time step. Finally, the aboveground density in each **quadrat** is updated.

Schedule details

The schedule follows the processes of the dewy-pine life cycle during a year from the annual census occurring in May. This census occurs during the flowering period and the model replicates this by starting with the *Reproduction* submodel. The *Survival and growth* and *Seedbank* submodels could come in any order after reproduction took place, as they are independent from each other.

In natural populations, the schedule depends on the fire regime. Reproduction does not happen until the second year after a fire occurs, and only survival and growth, as well as germination or dormancy in the seedbank, are represented in the year of a fire and the following year.

4. Design concepts

1. Basic principles

This model relies on previous knowledge on the life cycle of dewy pines (Paniw et al., 2017; Conquet et al., 2023) to perform a population viability analysis (PVA), a modelling approach commonly used in population ecology. By projecting population dynamics into the future, a PVA aims at assessing the probability of persistence of populations and allows for the introduction of stochasticity in environmental conditions (e.g. fire return, or sampling from a distribution of temperature and rainfall values). While this model is designed for plant populations and does not include any representation of social organisation or individual's decision processes, it allows to take into account demographic stochasticity (by sampling demographic processes from distributions), which is often unaccounted for in PVAs due to the use of simplified population models such as matrix population models (MPM) or integral projection models (IPM).

2. Emergence

Changes in aboveground population size emerge from individual fate, which in turn emerges from the relationship between demographic processes (e.g. survival or reproduction) and individual traits (plant size), density, and environmental variables. Individual traits and density vary with changes in demographic processes affecting individual fate. How the various demographic processes interact to shape individual life histories is imposed by previous empirical observations on the species' life cycle.

Seedbank processes emerge from the simulated sequence of post-fire habitat stages (in natural populations) or from site-specific parameters that do not vary through time parameters (in anthropogenic populations).

3. Adaptation

Individuals do not make any decisions based on objectives in this model.

4. Objectives

Individuals do not use any fitness measure to make decisions.

5. Learning

Learning is not implemented in this model.

6. Prediction

Prediction is not implemented in this model.

7. Sensing

Sensing is not implemented in this model.

8. Interaction

Interactions between individuals in this model are mediated by competition for resources (e.g. light or prey) and facilitation (e.g. provision of shade). These interactions are represented by the effect of density at the beginning of year *t* on demographic processes, and in turn individual fate, from time *t* to *t*+1. Here, density corresponds more specifically to the number of aboveground individuals of size > 4.5 in a given 1-m^2 quadrat, as we expect from observations that individuals further than the quadrat are too far to affect focal plants, and that smaller individuals only have a small effect on other individuals.

9. Stochasticity

Stochasticity occurs at several levels of the model. First, if the user chooses to project the population under current climatic conditions, the sequence of years of the desired length will be created by randomly sampling from the list of observed years. If the user chooses to project the population under future climate-change conditions, this random sampling of observed years is used to obtain the sequence of years to be used as random effects in the submodels, that is, the years representing the variation in demographic processes that is not explained by environmental conditions, individual traits, or density.

Additionally, all demographic processes governing the fate of both aboveground **plants** and **produced and seedbank seeds** are stochastic. For each **plant**, the survival, size (at the next time step or after germinating), flowering status, and

number of flowers are sampled from binomial, scaled Student *t*, and Poisson distributions with parameters obtained from predictions of generalised additive models and depending on the environmental conditions, individual traits, and density. For each **seed**, whether it germinates, stays dormant, or contributes to the seedbank is sampled from a binomial distribution with parameters depending on the site in which the simulation is performed or the time since last fire. The number of seeds per flower for each **plant** is sampled from a Poisson distribution with a fixed mean previously used in population projections for this system (Paniw et al., 2017; Conquet et al., 2023).

Moreover, the location of each seed in the seedbank at the start of the simulation is attributed randomly, with each quadrat having the same probability $\frac{1}{\text{total number of quadrats}}$ to be designated as a seed's location. In subsequent years, all **produced seeds** are assigned to the quadrat of the parent **plant**. This approach allows us to reproduce the lack of active dispersal mechanisms in dewy pines, leading most seeds to fall and establish next to the mother plant.

Finally, when the number of **plants** to add to the population is higher than the capping threshold set by the user, the new individuals to be removed from the recruits are sampled at random.

10. Collectives

There are no collectives in this model.

11. Observation

The two main outputs of this model are (1), for each simulation the yearly population growth rates (log $\lambda = \frac{N_t}{N_{t-1}}$, where N_t is the total population size—above ground and in the seedbank—in year t and $N_{t\text{-}1}$ in year t-1) that can be used to calculate the stochastic growth rate over the whole simulation (log $\lambda_S = \frac{\sum_{t=2}^{T} log\ \lambda_t}{T}$ where T is the number of simulated years), and (2) whether the population went extinct within the number of simulated years, which can be used to obtain the probability of quasi-extinction (proportion of simulations where the population went under the quasi-extinction threshold, i.e., 10 > aboveground individuals and 50 > seeds in the seedbank) across a number of simulations defined by the user.

In addition, the output of the model contains the full individual data across the whole simulation, the mean change in aboveground population abundance (i.e. the population growth rate without taking the seedbank into account), as well as population size and population density (i.e. number of individuals of size > 4.5 per 1-m^2 quadrat).

5. Initialization

For both habitats (natural and anthropogenic) and all scenarios (control and climate change) the initial number of aboveground **plants**, as well as their size and location (**quadrat**) corresponds to that observed in the population and first year chosen by the user for the simulation, as does the density in each **quadrat**. The number of **seeds** present in the seedbank when starting the simulation is defined by the user (by default 10,000 for natural populations and 3,000 for anthropogenic

240 populations), and the **seeds** are initially assigned randomly to their **quadrat**. The
241 number of **produced seeds** and the extinction status are initialised at 0. The
242 sequence of yearly population growth rates, mean change in aboveground
243 population abundance, and population density are initialised with NAs.
244
245 In both scenarios, the required number of years (set by the user) is sampled among
246 the years observed in the full individual data (e.g. 30 samples of years 2016–2021).
247 This sequence of years is used to represent random year variation (i.e., random
248 effects in vital-rate models). However, the sequence of yearly temperature and
249 rainfall values depends on the scenario. Under the control scenario, these values
250 correspond to the observed climate in each year of the sampled sequence. When
251 the population is projected under climate change, the temperature and rainfall values
252 reflect the projected climate values obtained from the global circulation models
253 (GCM) from the first year defined by the user and following a chronological order
254 until the end of the simulation.
255
256 Finally, projecting natural populations requires to initialise a sequence of post-fire
257 habitat stages (0–4). In the first year, this corresponds to the stage observed in the
258 first year of the simulation (defined by the user). The following stages are determined
259 by a Markov chain (Fig. S1; see also Paniw et al., 2017; Conquet et al., 2023), where
260 the transition from the last to the first stage (fire year) depends on the probability of
261 fire return (p), which is set by the user (1/30 by default). The sequence of number of
262 years since the last fire (TSF) is initialised using the observed number in the first

year of the simulation, with the subsequent TSFs being inferred from the sequence of post-fire habitat stages.

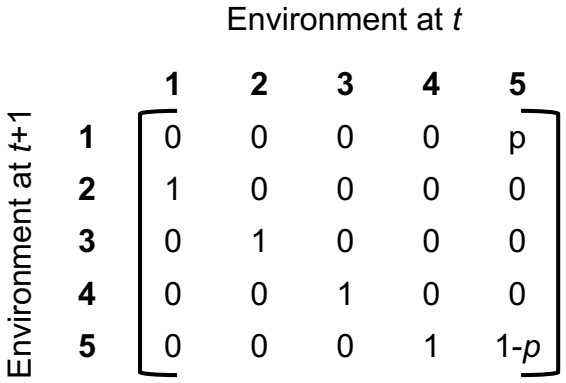

Figure S1 - Markov chain determining the succession of post-fire habitats for the dewy pine population. The first four states (from the fire year to the third year after a fire) constitute the deterministic part of the Markov chain and thus always follow each other in a sequence of 1 to 4 (probability of transition = 1). The fifth state (from the fourth year after a fire) is stochastic, and the transition from this state depends on the fire frequency *p* (i.e., the population will remain in state 5 until a fire occurs).

6. Input data

The model uses as input data individual-based data on dewy pines (aboveground **plants)** in the population chosen by the user. These data have been collected during annual population surveys occurring in May since at least 2016 (earlier for some populations, see Appendix S2). These surveys enabled us to obtain data on individuals' survival, size (log[length of the longest leaf x number of leaves]), reproductive status, and number of flowers (Paniw et al.,, 2017). Additionally, the model uses input data containing values from 2016 to 2050 of (1) average daily

minimum temperature (in ºC) in summer and fall following a census and fall and winter prior to a census, and (2) cumulative rainfall (in mm) in fall and winter following a prior to a census. Details on data sources and preparation can be found in Appendix S2.

7. Submodels

Reproduction

Flowering: Individuals can reproduce from two years after a fire occurred in natural populations (Paniw et al., 2017). The reproductive status of individuals (0 or 1) is drawn from a binomial distribution which probability is predicted from a generalised additive model (GAM) describing the observed relationship between flowering probability and winter mean daily maximum temperature, fall cumulative rainfall, individual size, aboveground density of individuals with size > 4.5, and time since last fire in natural populations (see Appendix S1: Table S5 for the full equation linking the various covariates to flowering probability).

Number of flowers per individual: Reproductive individuals (i.e., flowering = 1) can produce flowers, their number being drawn from a negative binomial distribution which probability is predicted from a generalised additive model (GAM) describing the observed relationship between the number of flowers and winter mean daily maximum temperature, individual size, and time since last fire in natural populations (see Appendix S1: Table S5 for the full equation linking the various covariates to the number of flowers per individual).

Number of seeds per flower: The number of seeds for each flower is drawn from a Poisson distribution with a mean fixed at 9.8, which corresponds to the value used in previous population projections of the dewy-pine system (Paniw et al., 2017; Conquet et al., 2023).

Survival and growth

Survival: Individual survival (0 or 1) is sampled from a binomial distribution which probability is predicted from a generalised additive model (GAM) describing the observed relationship between survival and summer mean daily maximum temperature, fall cumulative rainfall, individual size, aboveground density of individuals with size > 4.5, and time since last fire in natural populations (see Appendix S1: Table S5 for the full equation linking the various covariates to survival).

Growth: The size of surviving individuals in the following year is sampled from a truncated scaled Student *t* distribution with location (i.e. mean), scale (i.e. standard deviation) and degrees of freedom obtained from a generalised additive model describing the observed relationship between individuals' size in the next year and fall cumulative rainfall, individual size, aboveground density of individuals with size > 4.5, and time since last fire in natural populations (see Appendix S1: Table S5 for the full equation linking the various covariates to growth). The minimum or maximum observed sizes were assigned to individuals with infinite size values.

Seedbank

Continuous germination and contribution to the seedbank: For each **produced seed**, whether it germinated directly without going to the seedbank (0 or 1) was sampled from a binomial distribution with a mean determined by the probability to germinate when produced (goCont) which depended on time since last fire (in natural populations) or site (in anthropogenic populations) (see Appendix S1: Table S1 for details on the mean values). Among the seeds that will not germinate, seeds that will contribute to the seedbank in the next year (0 or 1) were then sampled from a binomial distribution with a mean determined by 1-goCont. The rest of the seeds were considered dead and removed from the population. In anthropogenic populations, the probabilities of continuous germination and contribution to the seedbank were corrected for seed survival (i.e., multiplied by 0.33) and, in one population (Sierra Carbonera Disturbed), further multiplied by 0.4 to replicate more accurately the observed population dynamics.

Germination from the seedbank: For each **seedbank seed**, whether it germinated from the seedbank (0 or 1) was sampled from a binomial distribution with a mean depending on time since last fire (in natural populations) or site (in anthropogenic populations) (see Appendix S1: Table S1 for details on the mean values). In anthropogenic populations, the probability of germination from the seedbank was corrected for seed survival (i.e., multiplied by 0.33) and, in one population (Sierra Carbonera Disturbed), further multiplied by 0.4 to replicate more accurately the observed population dynamics.

Dormancy: For each **seedbank seed**, whether it remained dormant in the seedbank (0 or 1) was sampled from a binomial distribution with a mean depending on time since last fire (in natural populations) or site (in anthropogenic populations) (see Appendix S1: Table S1 for details on the mean values). In anthropogenic populations, the probability of dormancy was corrected for seed survival (i.e., multiplied by 0.33) to replicate more accurately the observed population dynamics.

Seedling size: The size of a germinating seed is sampled from a truncated scaled Student *t* distribution with location (i.e. mean), scale (i.e. standard deviation) and degrees of freedom obtained from a generalised additive model describing the observed relationship between seedling size and winter mean daily maximum temperature, aboveground density of individuals with size > 4.5, and time since last fire in natural populations (see Appendix S1: Table S5 for the full equation linking the various covariates to seedling size). The minimum or maximum observed sizes were assigned to individuals with infinite size values.

References – Appendix S3

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