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# Comparative Life-Cycle Analyses Reveal Interacting Climatic and Biotic Drivers of Population Responses to Climate Change


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## Abstract

Responses of natural populations to climate change are driven by how multiple climatic and biotic factors affect survival and reproduction, and ultimately shape population dynamics. Yet, despite substantial progress to synthesize the sensitivity of populations to climatic variation,

comparative studies still overlook such complex interactions among drivers that generate variation in population-level metrics. Here, we use a common framework to synthesize how the joint effects of climate and biotic drivers on different vital rates impact population change, using unique long-term data from 41 species, ranging from trees to primates. We show that simultaneous effects of multiple climatic drivers exacerbate population responses to climate change, especially for fast-lived species. However, accounting for density feedbacks under climate variation buffers the effects of climate-change on population dynamics. In all species considered in our analyses, such interactions among climate and density had starkly different effects depending on the age, size, or life-cycle stage of individuals, regardless of the life-history of species. Our work provides the first general framework to assess how covarying effects of climate and density across a wide range of population models can impact populations of plants and animals under climate change.

**Significance statement:** There is a growing consensus that complex interactions among vital rates and numerous abiotic and biotic drivers complicate simple predictions of climate-change impacts on plant and animal populations. Here, we use a unique dataset of some of the longest studied populations of 41 plant, bird, and mammal species to compare the effects of such complex mechanisms on population persistence. Despite the unique context of each study population, our results show remarkable generalizable patterns of population responses to climate variation. To advance future research, we provide fully reproducible models and an open-access data repository, enabling broad-scale integration of demographic responses to climate change.

## MAIN TEXT

### Introduction

Among the multiple challenges for biodiversity conservation, the increasing severity of climate change, interacting with other global-change drivers, is of particular concern (1). Inferring general patterns of how populations of plants and animals respond to such complex interactions, beyond single case studies, is a priority for theoretical and applied research and management (2). All populations in natural communities are structured by variation in genetic and phenotypic traits, and often also developmental stages, which determine how different rates of survival and reproduction are spread throughout the life cycle (3). In structured populations, climatic effects on population abundances are then filtered by how different biotic and abiotic drivers (including climate) affect trait-, age-, or stage-specific survival and reproduction (4-13). For instance, population persistence may be particularly affected when several climatic factors simultaneously reduce survival and reproduction of several life-cycle stages, accelerating population decline (5). In particular compound effects of hotter and drier climatic conditions on individuals are projected to increase under climate change and can have strong negative impacts on natural populations and communities (14,15), especially in combination with land-use change (16). However, populations may also be buffered from adverse climatic effect, when vital rates with higher impact on population growth, i.e., adult survival, exhibit the least temporal variability and thus stabilize population fitness (18, 22-24). Furthermore, a decrease in one vital rate under climate stress (e.g., recruitment) can be compensated with increases in other vital rates, such as survival of the remaining recruits or adults, under negative density feedbacks (6,7, 20). This occurs because, when individuals compete for resources, negative climatic effects on hetero- or conspecific abundance will also ease competition (6, 26), which can allow the populations to recover faster from or show higher resilience to adverse climatic effects (27). The role of density dependence may be particularly important in assessing climate-change effects on population dynamics (26). Therefore, to broadly understand the impacts of climate change in complex natural systems, we need to understand how intrinsic and interspecific mechanisms interact to mediate such impacts on natural populations (28, 29).

Despite substantial progress to synthesize the sensitivity of populations to climatic variation, comparative studies have largely overlooked complex mechanisms of interacting drivers and vital rates that generate variation in population-level metrics. For instance, previous studies have linked global indices of temperature and rainfall to abundances or population growth rates to show that terrestrial populations of plants and animals with shorter generation times are relatively more sensitive to climatic variation (21, 30). Despite producing important insights, such analyses have not investigated vital-rate responses to multiple climatic factors and did not consider biotic drivers such as density dependence. A recent study compared the relative effect on plant population growth rates of perturbing abiotic vs. biotic drivers, but did not assess how simultaneous effects of different drivers on different vital rates affect populations (31). This contrasts with the growing consensus that complex interactions among vital rates and biotic and climatic drivers complicate projections of persistence under climate change (28, 32-36).

We synthesize, for the first time, how interacting climatic and biotic drivers change population dynamics across taxa by affecting different vital rates such as reproduction and juvenile and adult survival. Given the evidence for the importance of the effects of multiple abiotic drivers and their interactions with density feedbacks on population dynamics (5-12), we hypothesized that, generally, the simultaneous effects of several climatic drivers in vital-rate models amplify population responses to climate change; but that climate-change impacts on populations are buffered when intra- or interspecific density dependence is incorporated in vital-rate models.

We reviewed the ecological literature and identified studies that quantitatively linked at least two climatic drivers or one climatic and one biotic driver to at least two vital rates. Following (33), we defined climatic drivers as direct measures of temperature or precipitation, i.e., not drivers that affected climate indirectly, such as the Southern Annular Mode (i.e., *Catharacta lönnbergi* from (37); see *Supplementary Materials* for a complete list of selection criteria). Among the biotic drivers, we distinguished intraspecific interactions (e.g., density dependence, social interactions) and interspecific interactions (e.g., competition, food availability, predation, diseases). We then built structured population models and used them to compute sensitivities of population growth rates (38) to a given climatic driver, either accounting for simultaneous effects of all other drivers on vital rates or keeping other drivers fixed, thus reducing the complexity of environmental effects. We also compared the effects of perturbing different single vital rates to understand whether population-level sensitivities are driven by changes in specific vital rates across species. When testing our hypothesis, we controlled for potential confounding factors, most importantly the life-history strategy of populations, which has been shown to strongly mediate population responses to environmental change (19, 21). We created a database making all data and code freely available online, to allow researchers to link age- or stage-specific vital rates to population responses under environmental change for further analyses such as forecasts.

## Results

We extracted data from 23 studies including 41 species (15 birds, 8 mammals, and 18 plant species). Among these species, 18 matrix population models, eight integral projection models, five integrated population models, and 10 individual-based models were used, and vital rates were typically modeled using generalized linear models. Among biotic drivers, intraspecific density dependence was most commonly included as a driver in vital-rate models (i.e., in 13 studies; four birds, six mammals, three plants), while interspecific interactions were considered in only four cases. For an overview of life-history strategies, covariates, and demographic status of the species included in this comparative study, see Table S7. For each species, we calculated the scaled absolute sensitivities (|S|), i.e., changes in the population growth rate, $\lambda$, to observed climatic variation (standardized differences between maximum and minimum climatic values)

(31). In most studies, we calculated λ for either a single (meta)population or a representative average population across the habitat range, as in the case of eight bird species (39) and 11 Mediterranean tree species (40) – that is, vital-rate models did not distinguish populations explicitly. However, three studies (see Supplementary Materials) modeled vital-rate responses to climatic and biotic drivers that differed among populations. Here, we averaged sensitivities across populations to calculate species-specific average sensitivities to climate comparable across species (31). Additional analyses showed that such averaging did not affect results (Table S4). We also repeated analyses excluding these three studies altogether; this did not affect our results either (Table S5).

We modeled the variation in |S| using a modified meta-regression approach (41), where we pooled the results from all studies into one generalized linear hierarchical model. Our model included average age at maturity, a proxy for the fast-slow continuum of life-history strategies (42). As expected, slower-paced species had lower absolute sensitivities of λ (|S|) to climatic drivers compared to faster-paced species (Fig. 1; Table 1; $\beta_{Maturity} = -1.13 \pm 0.19$). These patterns agree with theoretical expectations (i.e., demographic buffering hypothesis (18, 25)) and previous empirical studies (19, 21, 30, 43) and suggest that fast-paced life histories across taxa are more labile to, or track, climatic fluctuations, whereas slow-paced life histories buffer population dynamics from multiple climatic effects (18, 19, 21).

Population responses to multiple climatic drivers and density dependence

Across life histories, sensitivities |S| to changes in a focal climatic driver were consistently higher when covarying climatic drivers were also perturbed than when holding other climatic drivers constant (Table 1; $\beta_{NoCovariation} = -0.25 \pm 0.11$; Table 1; Fig. 1). Thus, synergistic effects of different climatic drivers can have a stronger impact on population dynamics than considering the effects of such drivers in isolation, as is typically done in sensitivity analyses. At the same time, |S| were lower for populations where intraspecific density dependence explicitly affected vital rates along with climatic drivers, as opposed to populations that did not consider how climatic drivers interact with density dependence ($\beta_{DensityYes} = -1.00 \pm 0.56$; Table 1; Fig. 1; Fig. S1). These differences in including vs. excluding density dependence in population models were strongest when we accounted for the full complexity of environmental effects in sensitivity analyses (Fig. S1). That is, |S| increased by holding density dependence constant when perturbing a climatic driver as opposed to adjusting for observed changes in intraspecific density when the focal perturbed climatic driver was at its minimum and maximum ($\beta_{NoCovariation:Density} = 0.40 \pm 0.19$).

This suggest that covariation between climate and density may be critical in moderating climate-change impacts on populations across a wide range of taxa (5-12, 44, 45). Additional analyses further isolating the effects of density feedbacks vs. different biotic and abiotic drivers in vital-rate models confirmed that covariation with density lowered |S| when climatic drivers were perturbed (Fig. S2).

Demographic pathways of climate effects on populations

We perturbed climatic drivers in each vital-rate model separately for 26 species to understand how different vital rates mediate the sensitivity of λ (|S|) to these drivers. For the remaining species, we could not perturb single vital rates due to the complexity of the models. A generalized linear regression model revealed that fast-paced life histories, i.e., ones with a lower age at maturity (43), were relatively more sensitive to climate perturbations in reproduction and survival of non-reproductive individuals than slow-paced life histories (Table 2; Fig. S5). This is to be expected as reproduction contributes relatively more to population dynamics of fast-paced species (19). Our results provide further evidence that fast-paced life histories buffer critical vital rates from climatic perturbations less than slow-paced ones (18, 19, 22,23), because they have a higher energy budget that they can invest into growth, reproduction, or dispersal after perturbations (46). However, a closer look at sensitivities of λ to vital-rate specific effects of climatic drivers revealed a complex picture (Fig. 2). Across life histories, λ can be equally affected by perturbations in several vital rates, and some vital rates showed strong responses to one environmental variable, but weak responses to other variables (Fig. 2; Figs. S9 – S38).

Overall, our results showed that growth-rate sensitivities, |S|, varied substantially among species/studies (Table 1; Table 2). While the fixed and random effects in our GLMMs jointly explained > 80 % of the variance in |S|, the proportion of variance attributed to random effects was always relatively higher (see Tables S1-S5; Fig. S3). The effect of species explained > 50 % of the random variation in the model. We also note that while 20 studies included only one species, three modeled several species, and we could not completely separate species and study effect - attempting to do so resulted in overparameterized random effects. Although we accounted for potential variables that may have confounded our results, i.e., number of vital rates modeled and average number of parameters per vital rate, one reason for such high variance among species or studies may be the varying complexity among studies in model design or the specific climatic variable considered – complexity that we could not account for as independent covariates in our analysis. On the other hand, high variability in responses to environmental drivers among species have also been observed in recent studies (30, 33, 47, 48). Thus, while we can discern generalizable patterns in population responses to climatic perturbations, only the inclusion of a wider range of future studies can disentangle the complex sources of context-dependent variation in population dynamics.

## Discussion

Natural populations of plants and animals are increasingly affected by climate change worldwide (49, 50). By identifying under what context populations are more susceptible to negative effects of climatic drivers, we can prioritize conservation efforts and develop targeted strategies to mitigate adverse effects. Our comparative analyses shed light on some common demographic pathways through which populations of plants, mammals, and birds respond to complex interactions of climatic and biotic drivers. We show that simultaneous effects of multiple climatic drivers increase population sensitivity to climate change, while interactions between density dependence and climate can effectively lower such sensitivity. Our results thus have important implications for assessing how resilient populations are to climate change. They suggest that, in cases in which we know that multiple climate drivers influence vital rates, measuring the effect of only one of these climatic drivers on population dynamics likely overestimates its effects; while omitting how climate interacts with density feedbacks can substantially underestimate indirect effects of climate on populations.

Recent studies have emphasized that future climate risks to natural populations and humans will be exacerbated by compound effects of climate drivers (1, 51). While previous research has focused on understanding such compound effects on single species or populations (e.g., reviewed in 30, 34, 52), our results provide the first comparative evidence across different contexts that synergistic effects of different climatic drivers can have a strong impact on population dynamics. Compound climatic effects, such as low rainfall and high temperature, often constitute climatic extremes, e.g., hot droughts (51) and are becoming increasingly common (1). Such extremes can have strong, non-additive effects on physiological processes of plants (53) and animals (54), negatively affecting population dynamics (5, 32, 55). In meerkats (*Suricata suricatta*), for instance, extreme heat in a relatively dry rainy season can lead to substantial loss of body mass and increased risks of deadly disease outbreaks (56). We note, however, that our study assessed changes in the magnitude, but not in the direction of population responses to perturbations in climate. Therefore, compound effects such as unusually warm and rainy reproductive seasons, may also lead to strong increases in population growth (56), particularly for fast life histories (25, 57).

Climatic factors do not affect populations in isolation; other abiotic and biotic factors also play a role, and their impacts vary among populations and individuals within those populations (34, 58). Our results suggest that across taxa, adverse climate effects can be buffered by decreasing the number of individuals in a population and thus easing the effects of intraspecific density, when present in populations (5, 7). In turn, for populations that increase in abundance under climate change, a resulting stronger effects of negative density dependence may increase population fluctuations under adverse environmental conditions (36). Other studies have also demonstrated the importance of density feedbacks in regulating population responses under land-use change (59) or disease outbreaks (60, 61), while populations of some social species that show non-linear responses to population densities may be particularly susceptible to climate change if adverse climatic effects reduce optimal densities (5). Similarly, climate change also affects populations through changes in interspecific interactions such as predation, competition, or facilitation (12, 62). However, interspecific interactions are still very rarely explicitly modeled when projecting population dynamics (33), including in the studies used in our meta-analysis.

Despite this growing evidence on the importance of assessing interactions of abiotic and biotic effects when quantifying population persistence under climate change (4, 5, 13, 31, 33), such assessments are challenging. Unlike climatic variables that are often included as continuous covariates in vital-rate models and are easily perturbed, interactions with individuals of the same population or even different species took on many complex forms in the population models we used in this study. Some studies only included indirect or static measures of biotic effects. For example, the tree species in our analysis had a colonization factor in their models, which was indirectly related to density, but was decoupled from climate variables in vital rates (40). Similarly, the models of *Certhia familiaris*, *Linaria cannabina*, *Lophophanes cristatus*, *Prunella collaris*, *Prunella modularis*, *Pyrrhula pyrrhula*, *Sitta europaea*, and *Turdus torquatus* did not contain density as a continuous driver in their vital-rate models (which was required for our sensitivity analyses), but density served as a fixed species-specific parameter affecting fecundity (39). Thus, we could only assess the effects of covariation between climate and density dependence in 13 of the 41 modeled species. Although they represented all three taxonomic groups and covered a wide range of life histories, resulting in an unbiased sample, understanding whether density feedbacks are a general mechanism that moderates population fluctuations under climate change for a wider range of taxa requires broadening comparative analyses that can account for complex density effects.

Density feedbacks are not equally important in all populations (64), and their effects have been tested and considered to not substantially affect population dynamics in the case of *Marmota flaviventer* and *Lavandula stoechas* (see Supporting Materials). However, the potential effects of density feedbacks have not been tested in many recent population model (33), likely due to a combination of lack of data and model complexity. In addition, most frameworks to predict biodiversity loss under global change do not explicitly model dynamic interactions between density and global-change drivers (65). We thus emphasize that including density feedbacks in the climate-demography models, for instance using population density or population size as a covariate in models (12, 36), may be key to understand how resilient natural populations are to climate change. If such feedbacks are not included due to data limitations or modelling constraints, our results suggest that it is important to at least discuss the potential implications of such omissions (66).

Ultimately, the effects of climate change on population dynamics are filtered by the strength and direction of driver effects on different vital rates, and how much the latter contribute to population dynamics (e.g., 4-13, 19, 22, 26, 32, 35-37). For any life history, even slow-paced ones where adult survival is the key vital rate driving population dynamics (19), changes in population growth were the results of complex effects of various drivers across different vital rates, showing high context dependence (13). Rainfall scarcity or extreme temperatures may differently affect individuals depending on the habitat, season, and life-cycle stage considered (e.g., 5, 32), or depending on how other species in a given community are responding to climate change (62). The complexity of the life cycle may also indicate how much a population is buffered from adverse environmental effects (52). Some species have dormant life-cycle stages that can protect populations from environmental fluctuations (62). Dispersal, which was modeled in some studies considered here (see Supplementary Materials), can stabilize decreasing populations and allow individuals to track new suitable habitats, and may itself be strongly mediated by climate (67). Therefore, from trees to primates, identifying how different abiotic and biotic factors impact populations across their full life cycle is key to be able to target conservation efforts towards certain factors during certain times of the life cycle.

Our work has advanced comparative demographic analyses in two important ways. First, we standardized sensitivity analyses across a wide variety of population models, ranging from classic matrix population models to integrated population and integral projection models, and individual-based models. By including the experts for each study system, we ensured that our methods did not produce inadvertent errors. Second, we provide a freely accessible and dynamic (i.e., constantly updated) database of population models that was compiled for this study. This offers an ideal basis to expand the number of studies and analyses in the future – for instance, forecasting how changes of local climatic drivers may affect populations and whether such effects can be approximated by global climate indices (68). We also recognize several limitations of our work. One limitation is that we could not account for taxonomic and geographical biases as we relied on available high-quality structured models that integrate multiple environmental factors (see *Supplementary Materials* for study-specific details). Such tailored models are available for specific terrestrial plants, mammals, and birds, but are still lacking for many invertebrate species (69,70), where relatively little is known on the demographic pathways through which climate change impacts abundance (71). We also have a geographic bias in our data as most study systems are from the Northern Hemisphere. Additionally, we only considered studies published in English. These types of biases can limit our ability to generalize patterns and employ conservation efforts based on comparative analyses (72, 73).

When searching the literature for appropriate studies, we also discovered that reproducibility of ecological studies remains a problem. Of the 76 studies that met our search criteria, we could only replicate population models of 24 %. For the remaining studies, data and code to replicate analyses were not freely available and could often not be reproduced even when in contact with authors. Thus, we emphasize that making not just data but also code available is an important step towards reproducible comparative analyses in ecology (74).

Our comparative analyses provide evidence that interactions among biotic and abiotic drivers, and the complex effects of such multiple drivers on different vital rates, hinder simplistic predictions of population persistence under climate change. We emphasize the need to recognize and incorporate interactions between climate and density dependence into full life-cycle models in order to understand and potentially mitigate the threat that climate change poses on natural populations.

## Materials and Methods

*Literature search*

Our main objective was to collect code and data from studies which (i) modeled vital rates (e.g., survival, growth, reproduction) in natural populations as a function of at least two climatic variables or one climatic and one biotic variable; and (ii) constructed structured population models from which population growth rates could be obtained. We focused on studies where data were obtained in natural, unmanipulated populations (i.e., discarding experimental studies); and where the environmental variables were continuous so that we could calculate means and standard errors (see equation 1). We therefore excluded studies that constructed models for good/bad, dry/wet environments, etc. To obtain suitable studies, we performed a targeted review of the literature. We first considered a recent review, which revealed a lack of understanding regarding comprehensive demographic responses to climate change for terrestrial mammals including 87 species (33) From the publications in this review, we selected those that met our criteria. To supplement data from this list of studies, we conducted a Web of Science search using the search terms from (33) and also checked the Padrino database (75) as well as (76) (Details in Supplementary Materials). To be included in our database, vital-rate models had to be reproducible, i.e., the regression models were fully reported, including their formula, coefficients, and standard errors. We were able to obtain data from 23 studies that met all these criteria.

As the first step of the analysis, we prepared a standardized protocol to build and perturb different structured population models, to maximize the ease of comparison across studies (https://doi.org/10.5281/zenodo.16992231). For help with conducting these analyses for the selected models, we contacted the authors of relevant studies. We extracted regression coefficients from tables to rebuild vital-rate models when possible; alternatively, the latter were provided by the authors of a given study. We then reconstructed population models from these vital rates, and the authors from the original papers reviewed these models to ensure that they were correct. In some cases, authors already provided the R code to rebuild the population model (for more information see Supplementary Materials). The environmental covariate data were also obtained from the authors of the papers. All studies built structured population models based on > 7 years of demographic data collection and/or using data across the distribution range of species, and the range of environmental covariate values was sufficient to robustly build and perturb structured population models (see Supplementary Materials on study-specific details).

Next, we compared among the species how perturbations in climatic variables affect long-term population fitness, λ, i.e., the sensitivity of λ to climatic drivers. For studies that provided matrix population models or integral projection models, we calculated λ as the annual asymptotic population growth rate using R package popbio (77) version 2.7. For studies that developed individual-based or integrated models, we calculated λ as the mean of annual growth rates over at least 50 years from at least 100 simulations (see Supplementary Materials for study-specific details; Figs. S38-S52). The approach of how λ was calculated did not affect our results (Table S3; Fig. S6). To obtain sensitivities of λ to climatic drivers, we calculated λ under minimum and maximum values of a climatic driver while (i) accounting for the actual observed values of other drivers when the focal driver was at its minimum or maximum (sensitivities with **covariation**) or (ii) holding the other drivers constant at their average values (sensitivities **without covariation**). When studies modeled random year effects consistently across vital rates, we set the years to ones where a climatic driver was at its minimum or maximum in analyses. We then calculated the scaled sensitivities according to Morris et al. (31) for each population and driver (Equation 1):

$$|S| = \left|\frac{\lambda_{max} - \lambda_{min}}{(d_{max} - d_{min})/\mathrm{SD}_d}\right| \quad \text{Equation 1}$$

The driver values $d_{max}$ and $d_{min}$ produced the population growth rates when the driver was set to its maximum value ($\lambda_{max}$) and its minimum value ($\lambda_{min}$). The denominator of the scaled sensitivity |S| is the difference in the driver levels in standard deviation (SD) units. The *scaled* sensitivity makes it possible to compare |S| across different studies and driver types (31). We calculated |S| for each climatic driver in vital-rate models (see *Sensitivity Analyses* in Supplementary Materials). We tested the robustness of the sensitivity metric by comparing |S| to the most common type of metric for summarizing outcomes in ecological meta-analyses: log response ratios (see *Alternative sensitivity parameterizations* in Supplementary Materials; Figs. S7-S8; Table S6).

We accounted for uncertainties around all |S| estimates by resampling parameters from vital-rate models and recalculating λ and |S| each time. More specifically, if a study reported the standard errors of the regression coefficients, we simulated the parameter distributions and sampled parameters from it, whereas in the case of Bayesian regressions, we sampled parameters from the MCMC posteriors. We produced 100 |S| estimates for most species but had to use fewer samples in some cases due to computational limits (see species-specific details in Supplementary

Materials). In three cases, we averaged |S| over different populations to get species-specific results. However, this averaging did not affect our overall conclusions (see Table S4).

Further, we perturbed the climatic drivers in each vital rate separately whenever possible (Figs. S12 – S38 for the specific vital rates in each species' model), in the same manner as above, to get vital-rate specific |S|. In this case, all environmental driver values covaried with the focal driver in the perturbed vital-rate but were held at their average values in other vital rates. Lastly, for populations (n =13) where intraspecific density dependence was explicitly considered as a driver in vital-rate models, we performed additional perturbations: We accounted for the actual observed values of other climatic or biotic drivers when perturbing a focal climatic driver (sensitivities with covariation), but held densities constant (i.e., did not account for covariation with density). We did this to test how much |S| depended on density dependence moderating the effects climatic changes.

*Statistical analyses*

We used a generalized linear mixed model (GLMM), assuming a Gamma distributed response under a log link function, to understand the underlying mechanisms influencing population-level sensitivities |S| to climate change. We chose the Gamma distribution because the scaled sensitivities were positive values larger than zero. The resulting model fit well to observed data (Fig. 1), and model fit was substantially better than using a log-normal distribution, based on AIC and residual plots (78). We included log(age at sexual maturity) as a continuous covariate for the effect of life-history speed on |S|. To test whether covariation among climatic drivers and lambda changed |S|, we incorporated as predictor variables: covariation with other drivers when λ was calculated under minimum/maximum values of a focal climatic driver (categorical; accounted for or not), intraspecific density effects (categorical; incorporated or not in vital-rate models), and the interaction between the two. We focused on intraspecific density effects to analyze the role of biotic interactions in population dynamics because this was the most common type of biotic variables included in vital rate models across species (see Table S7). We also controlled for a potential effect of model complexity on |S|, by including the log(number of vital rates) and log(mean parameters per vital rate) in each population model. Taxonomic groups and species were integrated as nested random effects on the model intercept to account for non-independent species-specific perturbations of different climatic drivers in vital-rate models. To account for differences among taxonomic groups and species in how much driver covariation affects |S|, the same nested random effects were also applied on the slope of the covariation variable. We also assessed whether |S| differed depending on which type of climatic driver was perturbed in vital-rate models (temperature vs. rainfall) by fitting another GLMM akin to the main analysis but including climatic driver as a covariate (Table S2; Fig. S4).

To better understand which vital rates were driving |S|, we repeated the GLMMs using |S| calculated by perturbing climatic drivers in single vital rates. To facilitate comparisons among species, we grouped the vital rates of each species into three main types: survival of non-reproductive individuals (including juveniles), survival of reproductive individuals, and reproduction (including reproductive success and recruitment). We excluded trait change (including growth and maturation) as a vital rate, as it was only modeled in four species: *Marmota flaviventer*, *Rhabdomys pumilio*, *Suricata suricatta*, and *Protea repens*. The resulting GLMM had a similar structure as the one for the global |S|, with two differences. First, as we calculated vital-rate specific |S| without simplifying driver covariation in specific vital rates, covariation was not included in the model. Second, as we held variables constant in non-perturbed vital rates, we simplified the model structure further by excluding whether species included or excluded density feedbacks in vital-rate and population models. We included main vital-rate type as a covariate and tested whether the climatic effects of different vital rates on |S| differed among life histories, via the effects of log(age at maturity), and used an interaction term of vital rate and age at sexual maturity.

We calculated marginal and conditional $R^2$ for all GLMMs to quantify the variance in the data explained by the fixed effects and random and fixed effects, respectively (79). We made all the data and code available online, along with the templates, ensuring that future analyses follow the same structure (https://doi.org/10.5281/zenodo.16992231).

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**Supplementary Materials:** Separate pdf file

**Table 1. Output of model assessing how age at sexual maturity, covariation with other drivers, presence of density feedbacks in vital-rate models and other covariates affected scaled sensitivities of population growth rates to changes in climate, |S|.**

| ***A* Fixed Effects** | **Coefficient** | **SE** | **P** |
|---|---|---|---|
| **Intercept** | -3.085 | 0.945 | **0.001** |
| **Covariation$_{no}$** | -0.250 | 0.112 | **0.026** |
| **Density$_{yes}$** | -1.004 | 0.556 | 0.070 |
| **Age at sexual maturity** | -0.991 | 0.200 | **<0.001** |
| **Number of vital rates** | -0.221 | 0.501 | 0.660 |
| **Parameters per vital rate** | 0.760 | 0.497 | 0.127 |
| **Covariation$_{no}$:Density$_{yes}$** | 0.470 | 0.192 | **0.014** |
| ***B* Random Effects** | Variance | SD | Prop. variance |
| **Species/Group (Intercept)** | 1.738 | 1.318 | 0.633 |
| **Species/Group Covariation$_{no}$** | 0.241 | 0.473 | 0.088 |
| **Group (Intercept)** | <0.001 | <0.001 | <0.01 |
| **Group Covariation$_{no}$** | <0.001 | <0.001 | <0.01 |
| **Residual** | 0.767 | 0.757 | 0.279 |
| **Marginal $R^2$ (variance explained by fixed effects): 0.300** | | | |
| **Conditional $R^2$ (variance explained by fixed and random effects): 0.829** | | | |

The fixed effects (A) and random effects (B) of the generalized linear mixed model with gamma log link are shown here. The coefficient, standard error (SE), and p-value are reported for each fixed effect, whereas variance and standard deviation (SD) are reported for each random effect, as well as prop. variance, which indicates the proportion of the total random-effect variance explained by different grouping variables. Nested random effects were incorporated due to multiple observations within species and groups ($n_{samples}$ = 17'240, $n_{species}$ = 41, $n_{groups}$ = 3). $n_{samples}$ reflects all resampled |S| for each perturbation scenario and species to account for parameter uncertainty. Bold p-values indicate statistical significance (α = 0.05).

**Table 2. Output of model assessing how age at sexual maturity, vital-rate type, presence of density feedbacks in vital-rate models, and other covariates affected scaled sensitivities of population growth rates to changes in climate, |S|, calculated by perturbing individual vital rates.**

| ***A* Fixed Effects** | **Coefficient** | **SE** | **P** |
|---|---|---|---|
| **Intercept** | -3.324 | 1.143 | **0.003** |
| **Vital rate$_{\text{non-reproductive survival}}$** | -0.620 | 0.385 | 0.107 |
| **Vital rate$_{\text{reproductive survival}}$** | 0.030 | 0.363 | 0.936 |
| **Age at sexual maturity** | -2.157 | 0.529 | **<0.001** |
| **Number of vital rates** | -0.738 | 0.564 | 0.191 |
| **Parameters per vital rate** | 0.850 | 0.541 | 0.117 |
| **Age at sex. mat.:vital rate$_{\text{non-reproductive survival}}$** | 1.412 | 0.596 | **0.012** |
| **Age at sex. mat.:vital rate$_{\text{reproductive survival}}$** | 1.097 | 0.491 | **0.025** |
| ***B* Random Effects** | Variance | SD | Prop. variance |
| **Species/Group (Intercept)** | 2.057 | 1.434 | 0.272 |
| **Species/Group Vital rate$_{\text{non-reproductive survival}}$** | 2.336 | 1.528 | 0.283 |
| **Species/Group Vital rate$_{\text{reproductive survival}}$** | 2.078 | 1.442 | 0.264 |
| **Group (Intercept)** | <0.001 | <0.001 | <0.01 |
| **Group Vital rate$_{\text{non-reproductive survival}}$** | <0.001 | <0.001 | <0.01 |
| **Group Vital rate$_{\text{reproductive survival}}$** | <0.001 | <0.001 | <0.01 |
| **Residual** | 0.957 | 0.998 | 0.180 |
| **Marginal $R^2$ (variance explained by fixed effects): 0.271** | | | |
| **Conditional $R^2$ (variance explained by fixed and random effects): 0.878** | | | |

The fixed effects (A) and random effects (B) of the generalized linear mixed model with gamma log link are shown here. The coefficient, standard error (SE), and p-value are reported for each fixed effect, whereas variance and standard deviation (SD) are reported for each random effect, as well as prop. variance, which indicates the proportion of the total random-effect variance explained by different grouping variables. Nested random effects were incorporated due to multiple observations within species and groups ($n_{samples} = 13'040$, $n_{species} = 26$, $n_{groups} = 3$). $n_{samples}$ reflects all resampled |S| for each perturbation scenario and species to account for parameter uncertainty. Bold p-values indicate statistical significance ($\alpha = 0.05$). Note that while perturbing one vital rate at a time, we accounted for covariation with other factors in the focal rate but set the covariates in the other vital-rate models to their mean values.

**FIGURE 1**

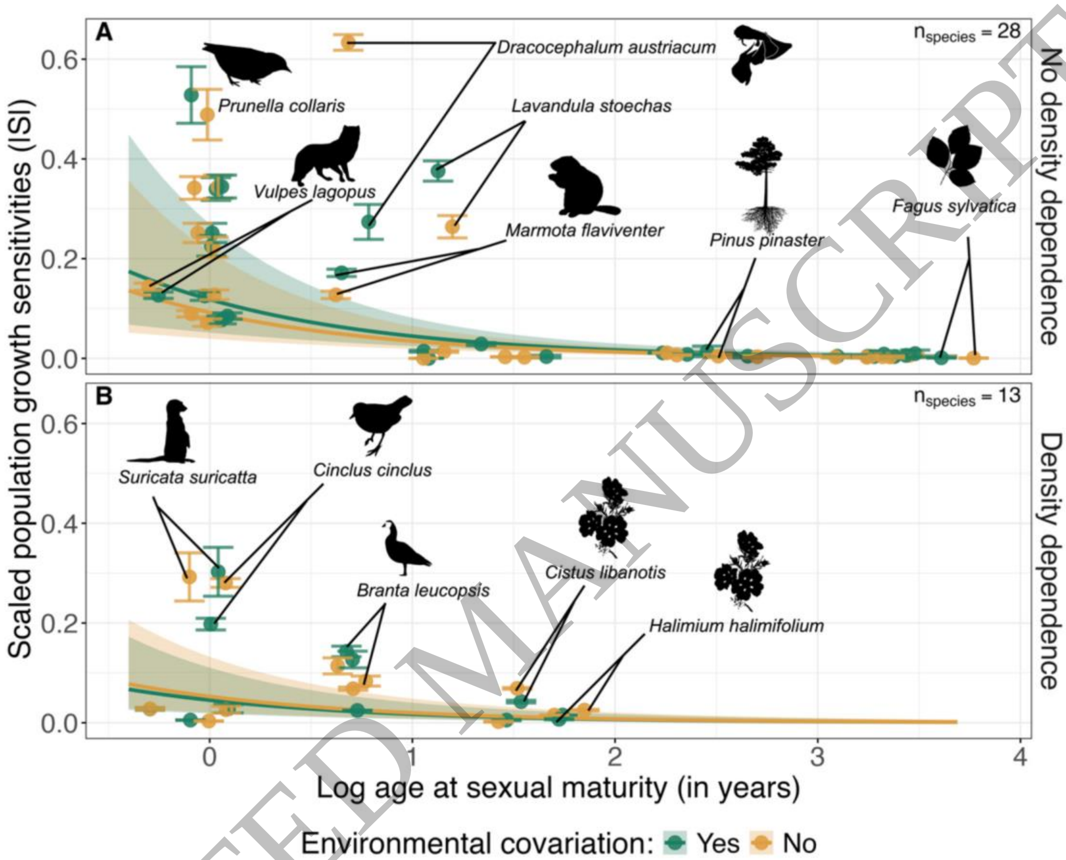


**Figure 1. Scaled sensitivities of population growth rates to climate, |S|, are lower when accounting for changes in population density under climate change**. Sensitivities are shown for species where density effects were not modeled explicitly (A) or were added (B) as covariates in vita-rate models. Different colors indicate sensitivity analyses under full environmental complexity (covariation with other drivers considered when perturbing a focal climate driver in vital-rate models) or reduced complexity (keeping other drivers as their average values when perturbing a focal driver). The lines represent predicted |S| over a range of ages of sexual maturity. The shaded areas indicate 95% model prediction intervals (see Table 1 for model coefficients). To aid visualization, the points show the observed sensitivity values of each species and perturbation scenario averaged over all perturbed climatic drivers and all resampled |S| under parameter uncertainty; with error bars showing the standard error. Figs. S9-S11 show the full distributions of resampled values per species. We labeled some example species across different life histories and taxa. Note that the points for a given species on the x axis are slightly separated so that error bars don't overlap.

*Figure 1*
*172x197 mm ( x DPI)*

# FIGURE 2

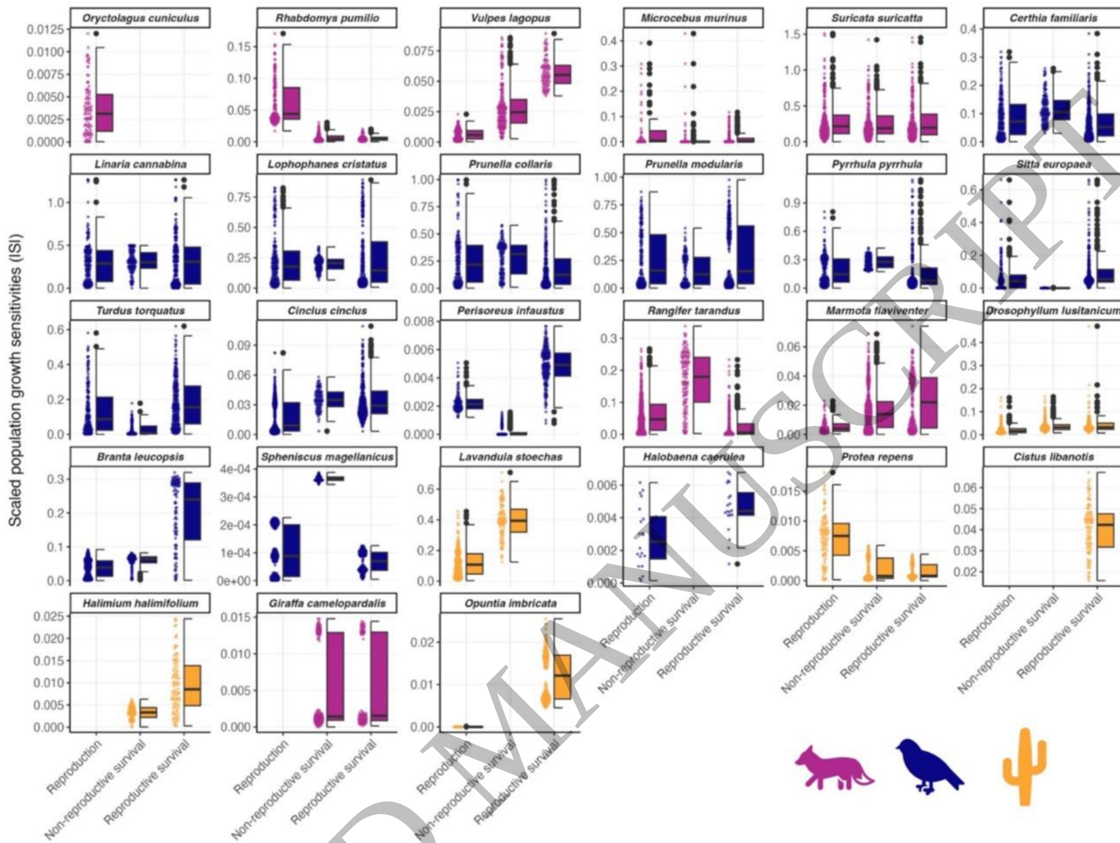


**Figure 2. For any species, scaled sensitivities of population growth rates (|S|) vary substantially when perturbing single vital rates**. Perturbations are shown for the species where we could perturb single vital rates. The plots are ordered by ascending age at sexual maturity and the colors indicate the taxa mammals, birds, and plants. The points represent |S| for each species, driver, vital rate, and parameter sample in vital-rate models. The boxplots display the distribution of |S|, including the median (central line), the interquartile range (box), and the range of the data (whiskers), with outliers shown as black points ($n_{\text{samples per species and vital rate}} = 100$, $n_{\text{sample for } \textit{Halobaena caerulea per vital} \text{ rate}} = 50$; see Supplementary Materials). If some sensitivities of some vital rates are missing, it's because these species did not have a climatic variable (but could have a biotic variable) in this specific vital rate.

*Figure 2*
*172x175 mm ( x  DPI)*