

1 **Main Manuscript for**

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

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116 **Author Contributions:** MP and AO developed the hypotheses, and EI refined them. EI led the
117 literature review, contacted the authors of studies (with help from MP) and standardized code for
118 this study. EC contributed substantially to the code development. EI wrote the first draft of the
119 manuscript, and MP edited and finalized the text. All authors contributed data and code for the
120 comparative analyses edited the manuscript. For a detailed contribution table, please see
121 <https://github.com/EsinIckin/Comparative-demography-project>.

122

123 **Abstract**

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

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

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

147

148 **MAIN TEXT**

149

150 **Introduction**

151

152 Among the multiple challenges for biodiversity conservation, the increasing severity of climate
153 change, interacting with other global-change drivers, is of particular concern (1). Inferring general
154 patterns of how populations of plants and animals respond to such complex interactions, beyond
155 single case studies, is a priority for theoretical and applied research and management (2). All
156 populations in natural communities are structured by variation in genetic and phenotypic traits,
157 and often also developmental stages, which determine how different rates of survival and
158 reproduction are spread throughout the life cycle (3). In structured populations, climatic effects on
159 population abundances are then filtered by how different biotic and abiotic drivers (including
160 climate) affect trait-, age-, or stage-specific survival and reproduction (4-13). For instance,

161 population persistence may be particularly affected when several climatic factors simultaneously
162 reduce survival and reproduction of several life-cycle stages, accelerating population decline (5).
163 In particular compound effects of hotter and drier climatic conditions on individuals are projected
164 to increase under climate change and can have strong negative impacts on natural populations and
165 communities (14,15), especially in combination with land-use change (16). However, populations
166 may also be buffered from adverse climatic effect, when vital rates with higher impact on
167 population growth, i.e., adult survival, exhibit the least temporal variability and thus stabilize
168 population fitness (18, 22-24). Furthermore, a decrease in one vital rate under climate stress (e.g.,
169 recruitment) can be compensated with increases in other vital rates, such as survival of the
170 remaining recruits or adults, under negative density feedbacks (6,7, 20). This occurs because,
171 when individuals compete for resources, negative climatic effects on abundance will also ease
172 competition (6, 26), which can allow the populations to recover faster from or show higher
173 resilience to adverse climatic effects (27). The role of density dependence may be particularly
174 important in assessing climate-change effects on population dynamics (26). Therefore, to broadly
175 understand the impacts of climate change in complex natural systems, we need to understand how
176 intrinsic mechanisms interact to mediate such impacts on natural populations (28, 29).

177

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

190

191 We synthesize, for the first time, how interacting climatic and biotic drivers change population
192 dynamics across taxa by affecting different vital rates such as reproduction and juvenile and adult
193 survival. Given the evidence for the importance of the effects of multiple abiotic drivers and their

194 interactions with density feedbacks on population dynamics (5-12), we hypothesized that,
195 generally, the simultaneous effects of several climatic drivers in vital-rate models amplify
196 population responses to climate change; but that climate-change impacts on populations are
197 buffered when density dependence is incorporated in vital-rate models.

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

214

215 **Results**

216

217 We extracted data from 23 studies including 41 species (15 birds, 8 mammals, and 18 plant
218 species). Among these species, 18 matrix population models, eight integral projection models,
219 five integrated population models, and 10 individual-based models were used, and vital rates
220 were typically modeled using generalized linear models. Among biotic drivers, intraspecific
221 density dependence was most commonly included as a driver in vital-rate models (i.e., in 13
222 studies; four birds, six mammals, three plants). For an overview of life-history strategies,
223 covariates, and demographic status of the species included in this comparative study, see Table
224 S6. For each species, we calculated the scaled absolute sensitivities ($|S|$), i.e., changes in the
225 population growth rate, λ , to observed climatic variation (standardized differences between
226 maximum and minimum climatic values) (31). In most studies, we calculated λ for either a single

227 (meta)population or a representative average population across the habitat range, as in the case of
228 eight bird species (39) and 11 Mediterranean tree species (40) – that is, vital-rate models did not
229 distinguish populations explicitly. However, three studies (see Supplementary Materials) modeled
230 different populations. Here, we averaged sensitivities across populations to calculate species-
231 specific average sensitivities to climate comparable across species (31). Additional analyses
232 showed that such averaging did not affect results (Table S4).

233

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

243

244 Population responses to multiple climatic drivers and density dependence

245

246 Across life histories, sensitivities $|S|$ to changes in a focal climatic driver were consistently higher
247 when covarying climatic drivers were also perturbed than when holding other climatic drivers
248 constant (Table 1; $\beta_{\text{NoCovariation}} = -0.25 \pm 0.11$; Table 1; Fig. 1). Thus, synergistic effects of
249 different climatic drivers can have a stronger impact on population dynamics than considering the
250 effects of such drivers in isolation, as is typically done in sensitivity analyses. At the same time,
251 $|S|$ were lower for populations where intraspecific density dependence explicitly affected vital
252 rates along with climatic drivers, as opposed to populations that did not consider how climatic
253 drivers interact with density dependence ($\beta_{\text{DensityYes}} = -1.00 \pm 0.56$; Table 1; Fig. 1; Fig. S1). These
254 differences in including vs. excluding density dependence in population models were strongest
255 when we accounted for the full complexity of environmental effects in sensitivity analyses (Fig.
256 S1). That is, $|S|$ increased by holding density dependence constant when perturbing a climatic
257 driver as opposed to adjusting for observed changes in intraspecific density when the focal
258 perturbed climatic driver was at its minimum and maximum ($\beta_{\text{NoCovariation:Density}} = 0.40 \pm 0.19$).
259 This suggest that covariation between climate and density may be critical in moderating climate-
260 change impacts on populations across a wide range of taxa (5-12, 44, 45). Additional analyses

261 further isolating the effects of density feedbacks vs. different biotic and abiotic drivers in vital-
262 rate models confirmed that covariation with density lowered $|S|$ when climatic drivers were
263 perturbed (Fig. S2).

264

265 Demographic pathways of climate effects on populations

266

267 We perturbed climatic drivers in each vital-rate model separately for 26 species to understand
268 how different vital rates mediate the sensitivity of λ ($|S|$) to these drivers. For the remaining
269 species, we could not perturb single vital rates due to the complexity of the models. A generalized
270 linear regression model revealed that fast-paced life histories, i.e., ones with a lower age at
271 maturity (43), were relatively more sensitive to climate perturbations in reproduction and survival
272 of non-reproductive individuals than slow-paced life histories (Table 2; Fig. S5). This is to be
273 expected as reproduction contributes relatively more to population dynamics of fast-paced species
274 (19). Our results provide further evidence that fast-paced life histories buffer critical vital rates
275 from climatic perturbations less than slow-paced ones (18, 19, 22,23), because they have a higher
276 energy budget that they can invest into growth, reproduction, or dispersal after perturbations (46).
277 However, a closer look at sensitivities of λ to vital-rate specific effects of climatic drivers
278 revealed a complex picture (Fig. 2). Across life histories, λ can be equally affected by
279 perturbations in several vital rates, and some vital rates showed strong responses to one
280 environmental variable, but weak responses to other variables (Fig. 2; Figs. S11 – S38).

281

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

295 generalizable patterns in population responses to climatic perturbations, only the inclusion of a
296 wider range of future studies can disentangle the complex sources of context-dependent variation
297 in population dynamics.

298

299 **Discussion**

300

301 Natural populations of plants and animals are increasingly affected by climate change worldwide
302 (49, 50). By identifying under what context populations are more susceptible to negative effects
303 of climatic drivers, we can prioritize conservation efforts and develop targeted strategies to
304 mitigate adverse effects. Our comparative analyses shed light on some common demographic
305 pathways through which populations of plants, mammals, and birds respond to complex
306 interactions of climatic and biotic drivers. We show that simultaneous effects of multiple climatic
307 drivers increase population sensitivity to climate change, while interactions between density
308 dependence and climate can effectively lower such sensitivity. Our results thus have important
309 implications for assessing how resilient populations are to climate change.

310

311 Recent studies have emphasized that future climate risks to natural populations and humans will
312 be exacerbated by compound effects of climate drivers (1, 51). While previous research has
313 focused on understanding such compound effects on single species or populations (e.g., reviewed
314 in 30, 34, 52), our results provide the first comparative evidence across different contexts that
315 synergistic effects of different climatic drivers can have a strong impact on population dynamics.
316 Compound climatic effects, such as low rainfall and high temperature, often constitute climatic
317 extremes, e.g., hot droughts (51) and are becoming increasingly common (1). Such extremes can
318 have strong, non-additive effects on physiological processes of plants (53) and animals (54),
319 negatively affecting population dynamics (5, 32, 55). In meerkats (*Suricata suricatta*), for
320 instance, extreme heat in a relatively dry rainy season can lead to substantial loss of body mass
321 and increased risks of deadly disease outbreaks (56). We note, however, that our study assessed
322 changes in the magnitude, but not in the direction of population responses to perturbations in
323 climate. Therefore, compound effects such as unusually warm and rainy reproductive seasons,
324 may also lead to strong increases in population growth (56), particularly for fast life histories (25,
325 57).

326

327 Climatic factors do not affect populations in isolation; other abiotic and biotic factors also play a
328 role, and their impacts vary among populations and individuals within those populations (34, 58).
329 Our results suggest that across taxa, adverse climate effects can be buffered by decreasing the

330 number of individuals in a population and thus easing the effects of intraspecific density, when
331 present in populations (5, 7). In turn, for populations that increase in abundance under climate
332 change, a resulting stronger effects of negative density dependence may increase population
333 fluctuations under adverse environmental conditions (36). Other studies have also demonstrated
334 the importance of density feedbacks in regulating population responses under land-use change
335 (59) or disease outbreaks (60, 61), while populations of some social species that show non-linear
336 responses to population densities may be particularly susceptible to climate change if adverse
337 climatic effects reduce optimal densities (5). Similarly, climate change also affects populations
338 through changes in interspecific interactions such as predation, competition, or facilitation (12,
339 62). However, interspecific interactions are still very rarely explicitly modeled when projecting
340 population dynamics (33).

341

342 Despite this growing evidence on the importance of assessing interactions of abiotic and biotic
343 effects when quantifying population persistence under climate change (4, 5, 13, 31, 33), such
344 assessments are challenging. Unlike climatic variables that are often included as continuous
345 covariates in vital-rate models and are easily perturbed, interactions with individuals of the same
346 population or even different species took on many complex forms in the population models we
347 used in this study. Some studies only included indirect or static measures of biotic effects. For
348 example, the tree species in our analysis had a colonization factor in their models, which was
349 indirectly related to density, but was decoupled from climate variables in vital rates (40).

350 Similarly, the models of *Certhia familiaris*, *Linaria cannabina*, *Lophophanes cristatus*, *Prunella*
351 *collaris*, *Prunella modularis*, *Pyrrhula pyrrhula*, *Sitta europaea*, and *Turdus torquatus* did not
352 contain density as a continuous driver in their vital-rate models (which was required for our
353 sensitivity analyses), but density served as a fixed species-specific parameter affecting fecundity
354 (39). Thus, we could only assess the effects of covariation between climate and density
355 dependence in 13 of the 41 modeled species. Although they represented all three taxonomic
356 groups and covered a wide range of life histories, resulting in an unbiased sample, understanding
357 whether density feedbacks are a general mechanism that moderates population fluctuations under
358 climate change for a wider range of taxa requires broadening comparative analyses that can
359 account for complex density effects.

360

361

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

374
375 Ultimately, the effects of climate change on population dynamics are filtered by the strength and
376 direction of driver effects on different vital rates, and how much the latter contribute to
377 population dynamics (e.g., 4-13, 19, 22, 26, 32, 35-37). For any life history, even slow-paced
378 ones where adult survival is the key vital rate driving population dynamics (19), changes in
379 population growth were the results of complex effects of various drivers across different vital
380 rates, showing high context dependence (13). Rainfall scarcity or extreme temperatures may
381 differently affect individuals depending on the habitat, season, and life-cycle stage considered
382 (e.g., 5, 32), or depending on how other species in a given community are responding to climate
383 change (62). The complexity of the life cycle may also indicate how much a population is
384 buffered from adverse environmental effects (52). Some species have dormant life-cycle stages
385 that can protect populations from environmental fluctuations (62). Dispersal, which was modeled
386 in some studies considered here (see Supplementary Materials), can stabilize decreasing
387 populations and allow individuals to track new suitable habitats, and may itself be strongly
388 mediated by climate (67). Therefore, from trees to primates, identifying how different abiotic and
389 biotic factors impact populations across their full life cycle is key to be able to target conservation
390 efforts towards certain factors during certain times of the life cycle.

391
392 Our work has advanced comparative demographic analyses in two important ways. First, we
393 standardized sensitivity analyses across a wide variety of population models, ranging from classic
394 matrix population models to integrated population and integral projection models, and individual-
395 based models. By including the experts for each study system, we ensured that our methods did

396 not produce inadvertent errors. Second, we provide a freely accessible and dynamic (i.e.,
397 constantly updated) database of population models that was compiled for this study. This offers
398 an ideal basis to expand the number of studies and analyses in the future – for instance,
399 forecasting how changes of local climatic drivers may affect populations and whether such effects
400 can be approximated by global climate indices (68). We also recognize several limitations of our
401 work. One limitation is that we could not account for taxonomic and geographical biases as we
402 relied on available high-quality structured models that integrate multiple environmental factors
403 (see *Supplementary Materials* for study-specific details). Such tailored models are available for
404 specific terrestrial plants, mammals, and birds, but are still lacking for many invertebrate species
405 (69,70), where relatively little is known on the demographic pathways through which climate
406 change impacts abundance (71). We also have a geographic bias in our data as most study
407 systems are from the Northern Hemisphere. Additionally, we only considered studies published in
408 English. These types of biases can limit our ability to generalize patterns and employ
409 conservation efforts based on comparative analyses (72, 73).

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

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

422

423

424 **Materials and Methods**

425

426 *Literature search*

427

428 Our main objective was to collect code and data from studies which (i) modeled vital rates (e.g.,
429 survival, growth, reproduction) in natural populations as a function of at least two climatic

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

444
445 As the first step of the analysis, we prepared a standardized protocol to build and perturb different
446 structured population models, to maximize the ease of comparison across studies
447 (<https://github.com/EsinIckin/Comparative-demography-project>). For help with conducting these
448 analyses for the selected models, we contacted the authors of relevant studies. We extracted
449 regression coefficients from tables to rebuild vital-rate models when possible; alternatively, the
450 latter were provided by the authors of a given study. We then reconstructed population models
451 from these vital rates, and the authors from the original papers reviewed these models to ensure
452 that they were correct. In some cases, authors already provided the R code to rebuild the
453 population model (for more information see Supplementary Materials). The environmental
454 covariate data were also obtained from the authors of the papers. All studies built structured
455 population models based on > 7 years of demographic data collection and/or using data across the
456 distribution range of species, and the range of environmental covariate values was sufficient to
457 robustly build and perturb structured population models (see Supplementary Materials on study-
458 specific details).

459
460 Next, we compared among the species how perturbations in climatic variables affects long-term
461 population fitness, λ , i.e., the sensitivity of λ to climatic drivers. For studies that provided matrix
462 population models or integral projection models, we calculated λ as the annual asymptotic
463 population growth rate using R package popbio (77) version 2.7. For studies that developed

464 individual-based or integrated models, we calculated λ as the mean of annual growth rates over at
465 least 50 years from at least 100 simulations (see Supplementary Materials for study-specific
466 details; Figs. S38-S52). To obtain sensitivities of λ to climatic drivers, we calculated λ under
467 minimum and maximum values of a climatic driver while (i) accounting for the actual observed
468 values of other drivers when the focal driver was at its minimum or maximum (sensitivities with
469 **covariation**) or (ii) holding the other drivers constant at their average values (sensitivities
470 **without covariation**). When studies modeled random year effects consistently across vital rates,
471 we set the years to ones where a climatic driver was at its minimum or maximum in analyses. We
472 then calculated the scaled sensitivities according to Morris et al. (31) for each population and
473 driver (Equation 1):

474
475

$$476 \quad |S| = \left| \frac{\lambda_{max} - \lambda_{min}}{(d_{max} - d_{min}) / SD_d} \right| \quad \text{Equation 1}$$

477

478 The driver values d_{max} and d_{min} produced the population growth rates when the driver was set to
479 its maximum value (λ_{max}) and its minimum value (λ_{min}). The denominator of the scaled sensitivity
480 $|S|$ is the difference in the driver levels in standard deviation (SD) units. The *scaled* sensitivity
481 makes it possible to compare $|S|$ across different studies and driver types (31). We tested the
482 robustness of the sensitivity metric by comparing $|S|$ to the most common type of metric for
483 summarizing outcomes in ecological meta-analyses: log response ratios (see *Alternative*
484 *sensitivity parameterizations* in Supplementary Materials).

485

486 We accounted for uncertainties around all $|S|$ estimates by resampling parameters from vital-rate
487 models and recalculating λ and $|S|$ each time. More specifically, if a study reported the standard
488 errors of the regression coefficients, we simulated the parameter distributions and sampled
489 parameters from it, whereas in the case of Bayesian regressions, we sampled parameters from the
490 MCMC posteriors. We produced 100 $|S|$ estimates for most species but had to use fewer samples
491 in some cases due to computational limits (see species-specific details in Supplementary
492 Materials). In three cases, we averaged $|S|$ over different populations to get species-specific
493 results. However, this averaging did not affect our overall conclusions (see Table S4).

494

495 Further, we perturbed the climatic drivers in each vital rate separately whenever possible (Figs.
496 S12 – S38 for the specific vital rates in each species' model), in the same manner as above, to get

497 vital-rate specific $|S|$. In this case, all environmental driver values covaried with the focal driver in
498 the perturbed vital-rate but were held at their average values in other vital rates. Lastly, for
499 populations ($n = 13$) where intraspecific density dependence was explicitly considered as a driver
500 in vital-rate models, we performed additional perturbations: We accounted for the actual observed
501 values of other climatic or biotic drivers when perturbing a focal climatic driver (sensitivities with
502 covariation), but held densities constant. We did this to test how much $|S|$ depended on density
503 dependence moderating the effects climatic changes.

504

505

506 *Statistical analyses*

507

508 We used a generalized linear mixed model (GLMM), assuming a Gamma distributed response
509 under a log link function, to understand the underlying mechanisms influencing population-level
510 sensitivities $|S|$ to climate change. We chose the Gamma distribution because the scaled
511 sensitivities were positive values larger than zero. The resulting model fit well to observed data
512 (Fig. 1), and model fit was substantially better than using a log-normal distribution, based on AIC
513 and residual plots (78). We included $\log(\text{age at sexual maturity})$ as a continuous covariate for the
514 effect of life-history speed on $|S|$. To test whether covariation among climatic drivers and λ
515 changed $|S|$, we incorporated as predictor variables: covariation with other drivers when λ was
516 calculated under minimum/maximum values of a focal driver (categorical; accounted for or not),
517 intraspecific density effects (categorical; incorporated or not in vital-rate models), and the
518 interaction between the two. We focused on intraspecific density effects to analyze the role of
519 biotic interactions in population dynamics because this was the most common type of biotic
520 variables included in vital rate models across species (see Table S6). We also controlled for a
521 potential effect of model complexity on $|S|$, by including the $\log(\text{number of vital rates})$ and
522 $\log(\text{mean parameters per vital rate})$ in each population model. Taxonomic groups and species
523 were integrated as nested random effects on the model intercept, respectively. To account for
524 differences among taxonomic groups and species in how much driver covariation affects $|S|$, the
525 same nested random effects were also applied on the slope of the covariation variable. We also
526 assessed whether $|S|$ differed depending on which type of climatic driver was perturbed in vital-
527 rate models (temperature vs. rainfall) by fitting another GLMM akin to the main analysis but
528 including climatic driver as a covariate (Table S2; Fig. S4).

529

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

545

546 We calculated marginal and conditional R^2 for all GLMMs to quantify the variance in the data
547 explained by the fixed effects and random and fixed effects, respectively (79). We made all the
548 data and code available online, along with the templates, ensuring that future analyses follow the
549 same structure (<https://github.com/EsinIckin/Comparative-demography-project>).

550

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1012

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1034 **Data and material availability:** All data and code are available on

1035 <https://github.com/EsinIckin/Comparative-demography-project>. All analyses are fully
1036 reproducible.

1037 **Supplementary Materials:** Separate pdf file

FIGURE 1

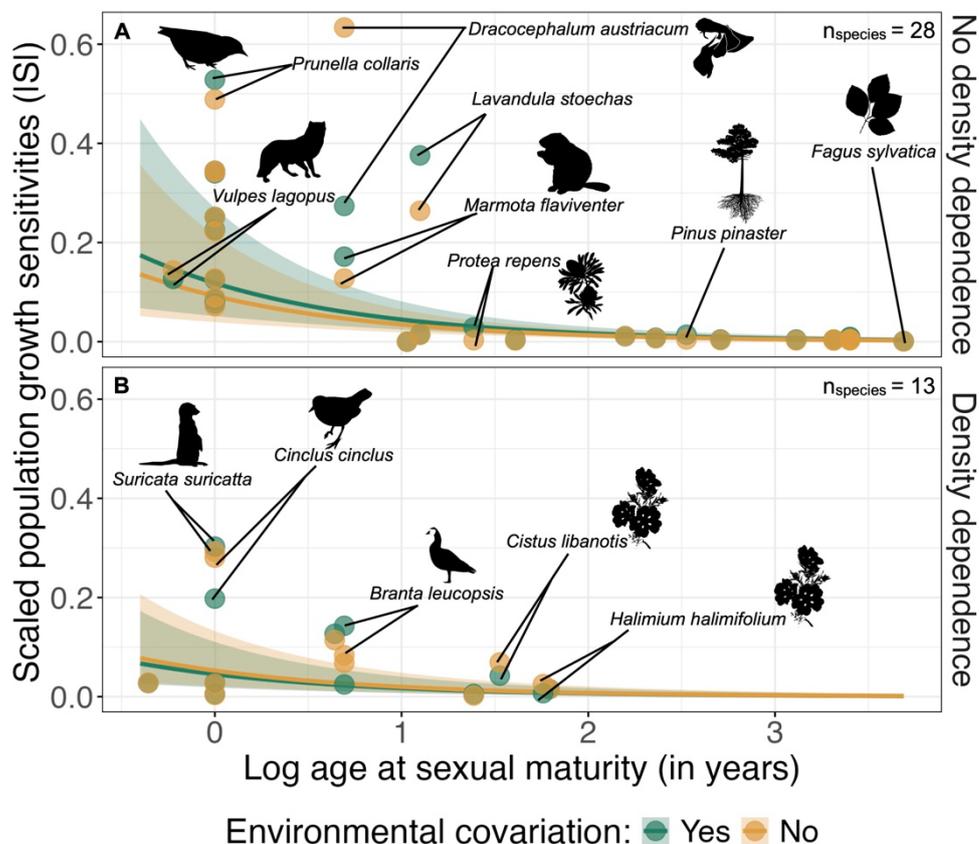


Figure 1. Scaled sensitivities of population growth rates to climate, $|S|$, are lower when accounting for changes in population density under climate change. Sensitivities are shown for species where density effects were not modeled explicitly (A) or were added (B) as covariates in vita-rate models. 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. Figs. S9-S11 show the distributions of resampled values per species. We labeled some example species across different life histories and taxa.

FIGURE 2

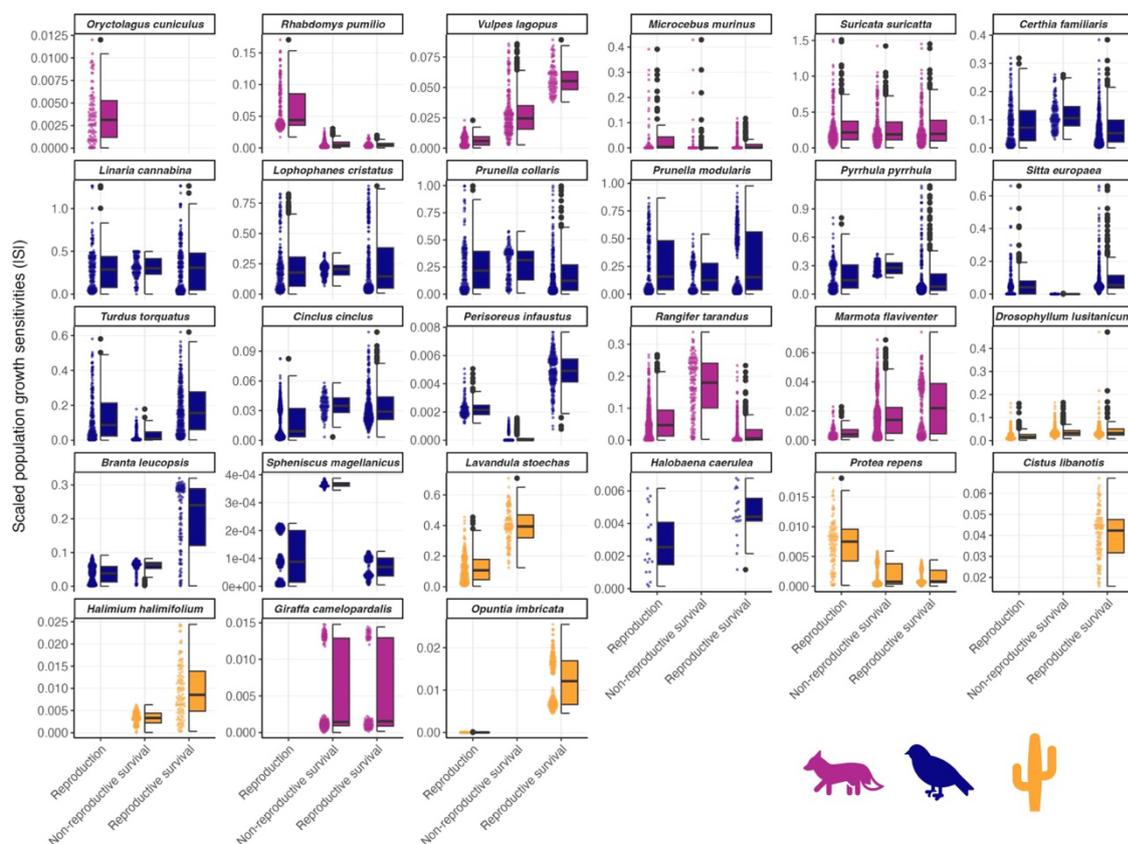


Figure 2. For any species, scaled sensitivities of population growth rates ($|S|$) vary substantially when perturbing single vital rates. Perturbations are shown for the species where we could perturb single vital rates. The plots are ordered by ascending age at sexual maturity and the colors indicate 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 ($n_{\text{samples per species and vital rate}} = 100$, $n_{\text{sample for Halobaena caerulea per vital rate}} = 50$; 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.

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|.

<i>A</i> 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
<i>B</i> 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 ($n_{\text{samples}} = 17'240$, $n_{\text{species}} = 41$, $n_{\text{groups}} = 3$). n_{samples} reflects all resampled |S| for each perturbation scenario and species to account for parameter uncertainty. Bold p-values indicate statistical significance ($\alpha = 0.05$).

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

<i>A</i> Fixed Effects	Coefficient	SE	P
Intercept	-3.324	1.143	0.003
Vital rate _{non-reproductive survival}	-0.620	0.385	0.107
Vital rate _{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 _{non-reproductive survival}	1.412	0.596	0.012
Age at sex. mat.:vital rate _{reproductive survival}	1.097	0.491	0.025
<i>B</i> Random Effects	Variance	SD	Prop. variance
Species/Group (Intercept)	2.057	1.434	0.272
Species/Group Vital rate _{non-reproductive survival}	2.336	1.528	0.283
Species/Group Vital rate _{reproductive survival}	2.078	1.442	0.264
Group (Intercept)	<0.001	<0.001	<0.01
Group Vital rate _{non-reproductive survival}	<0.001	<0.001	<0.01
Group Vital rate _{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

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

15