

Density feedbacks mediate effects of
environmental change on population dynamics of
a semi-desert rodent

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Abstract

1. Population dynamics are the result of an interplay between extrinsic and intrinsic environmental drivers. Predicting the effects of environmental change on wildlife populations therefore requires a thorough understanding of the mechanisms through which different environmental drivers interact to generate changes in population size and structure.
2. In this study, we disentangled the roles of temperature, food availability, and population density in shaping short- and long-term population dynamics of the African striped mouse, a small rodent inhabiting a semi-desert with high intra- and inter-annual variation in environmental conditions.
3. We parameterized a female-only stage-structured matrix population model with vital rates depending on temperature, food availability, and population density, using monthly mark-recapture data from 1609 mice trapped over 9 years (2005-2014). We then applied perturbation analyses to determine relative strengths and demographic pathways of these drivers in affecting population dynamics. Furthermore, we used stochastic population projections to gain insights into how three different climate change scenarios might affect size, structure, and persistence of this population.
4. We identified food availability, acting through reproduction, as the main driver of changes in both short- and long-term population dynamics. This mechanism was mediated by strong density feedbacks, which stabilized the population after high peaks and allowed it to recover from detrimental crashes. Density dependence thus buffered the population against environmental change,

and even adverse climate change scenarios were predicted to have little effect on population persistence (extinction risk over 100 years $< 5\%$) despite leading to overall lower abundances.

5. Explicitly linking environment-demography relationships to population dynamics allowed us to accurately capture past population dynamics. It further enabled establishing the roles and relative importances of extrinsic and intrinsic environmental drivers, and we conclude that doing this is essential when investigating impacts of climate change on wildlife populations.

Keywords

environmental drivers, environmental stochasticity, extrinsic, intrinsic, LTRE, matrix model, perturbation analysis, population dynamics, rodent, vital rate

1 Introduction

2 Contemporary climate change happens at a fast rate, and increases in temperatures
3 and the frequency of extreme events are predicted to continue (IPCC, 2014). Effects
4 of climate change on ecological systems have already become evident (Parmesan,
5 2006) and manifest themselves as alterations in species distributions (Chen *et al.*,
6 2011), shifts in phenology (Charmantier *et al.*, 2008), and changes in abundance
7 (Pounds *et al.*, 2006; Jepsen *et al.*, 2008). These impacts make it more impor-
8 tant than ever to understand and predict how climate affects life-history processes
9 and population dynamics of animals and plants both directly and indirectly (*e.g.*

10 through resource availability)(Williams *et al.*, 2002).

11 Population dynamics are the result of an interplay between different extrinsic
12 and intrinsic environmental factors (Stenseth *et al.*, 2002; Goswami *et al.*, 2011).
13 Extrinsic factors such as climate and resource availability interact with intrinsic
14 density feedbacks to generate variation in vital rates (survival, reproduction). Vi-
15 tal rate variation then translates into changes in population size and structure
16 (Leirs *et al.*, 1997; Lima *et al.*, 1999). The impacts of extrinsic environmental
17 factors and how these are affected by density may differ among seasons (*e.g.* Gul-
18 lett *et al.*, 2014), across species' life cycles (Gamelon *et al.*, 2017) and be subject
19 to stochastic variation among years, making population dynamics dependent not
20 only on current, but also on past conditions (Wilmers *et al.*, 2007). Predicting
21 potential impacts of climate change on species and ecosystems therefore requires
22 an in-depth understanding of how deterministic and stochastic variation in cli-
23 mate, resource availability, and density feedbacks jointly affect population dynam-
24 ics (Benton *et al.*, 2006; Boyce *et al.*, 2006). Such understanding can be gained
25 through quantitative models that explicitly link environmental factors to popula-
26 tion dynamics via vital rates (Ehrlén *et al.*, 2016) and the availability of long-term
27 individual-based data necessary to parameterize these models (Clutton-Brock &
28 Sheldon, 2010).

29 Collecting sufficient amounts of long-term individual-based data is easier for
30 species with short generation time, such as rodents. Rodent life histories are also
31 of particular interest because they are highly sensitive to the environment, and
32 consequently show large numerical fluctuations within and among years (Krebs,
33 2013). These fluctuations are of great ecological, social, and economical interest.
34 They are, for example, linked to ecosystem consequences of the dampening of vole

35 and lemming population cycles (Ims *et al.*, 2008; Schmidt *et al.*, 2012), stochas-
36 tic rodent eruptions with detrimental effects on crop production (Singleton *et al.*,
37 2010), and high risks of disease outbreaks (Gubler *et al.*, 2001). Rodents are also
38 often keystone species in food-webs and can function as ecosystem engineers (Kelt,
39 2011). Furthermore, while studying rodent populations - particularly in the con-
40 text of environmental change - is worthwhile in itself, drivers and mechanisms of
41 population dynamics may also be conserved across species. From a broader per-
42 spective, we may thus be able to use studies on easily accessible rodent systems
43 to gain valuable insights into general principles of population dynamics in variable
44 environments and to draw inferences about related or ecologically similar species
45 for which long-term individual-based data are not available (Frederiksen *et al.*,
46 2014).

47 Here, we study population dynamics of the African striped mouse (*Rhabdomys*
48 *pumilio*), a small rodent inhabiting a semi-arid ecosystem characterized by con-
49 siderable variation in timing and amount of annual rainfall and, consequently,
50 availability of green vegetation (Cowling *et al.*, 1999). Being adapted to such a
51 variable environment, the species displays high degrees of phenotypic plasticity
52 (Raynaud & Schradin, 2008; Nel *et al.*, 2015) and potentially large adaptive ca-
53 pacity in the face of environmental change (Rymer *et al.*, 2013). Variation in vital
54 rates of this rodent has previously been linked to temperature, food availability,
55 and population density (Nater *et al.*, 2016a). In this study, we re-analyse these
56 environment-demography relationships and link them to population dynamics in
57 a stage-structured population model. We then subject this model to retrospective
58 perturbation analysis to identify the roles and relative strengths of environmental
59 drivers in generating past population dynamics, and to prospective perturbation

60 analysis to investigate potential future responses of the African striped mouse to
61 alterations in the stochastic environment including different scenarios for future
62 climate change.

63 **Materials and methods**

64 **STUDY SYSTEM AND DEMOGRAPHIC DATA**

65 The African striped mouse (*Rhabdomys pumilio*) is a small murid rodent (adult
66 body mass of 30-85 g in the field) native to the dry regions of South Africa (Mal-
67 larino *et al.*, 2018). It is diurnal, forages alone but returns to a nest shared with an
68 extended family group at night (Schradin & Pillay, 2004). Group members share
69 one territory and interact amicably with each other, but are highly aggressive to-
70 wards striped mice from other groups (Schradin & Pillay, 2004). Striped mice are
71 omnivores, feeding primarily on the leaves of shrubs, small succulents and ephemerals,
72 but have also been observed to eat seeds and insects (Schradin, 2005). Home
73 range sizes vary strongly depending on local population density and seasonal food
74 availability (Schradin, 2006). The main breeding season is in the austral spring.
75 Most striped mice are therefore born between July and November, and can reach
76 sexual maturity after four weeks of age (Schradin & Pillay, 2014). However, they
77 often delay reproduction and remain in their natal territory until the breeding
78 season of the following year and few mice survive to a another breeding season
79 after that (life expectancy rarely exceeds 2 years, Schradin *et al.* (2012)).

80 The study population of African striped mice is located in the Goegap Nature
81 Reserve in the Succulent Karoo of South Africa (29°41' S, 18°01' E; altitude 912 m),
82 a semi-arid winter-rainfall ecosystem with marked vegetation peaks in spring. The

83 study population has been monitored since 2004 with a monthly capture-mark-
84 recapture program (trapping protocol described in detail in Schradin (2006)). For
85 this study, we assigned female striped mice to one of three life stages based on age
86 and reproductive status. Individuals below the age of four weeks were considered
87 immatures, while those that were older than four weeks but had not yet shown
88 signs of reproduction were assumed to be philopatrics (pre-reproductive adults).
89 Striped mice displaying a perforated vagina in month t-1, and/or signs of lactation
90 in month t were considered breeders (reproductive adults) from month t onwards
91 (Figure 1).

92 ENVIRONMENTAL DATA

93 To investigate environmental effects on vital rates and population dynamics of
94 striped mice, we explicitly included ambient temperature, food availability, and
95 adult population density into our analyses.

96 Monthly mean temperature represents a key seasonal cue, and was calculated
97 by averaging over daily measurements of minimum and maximum temperatures
98 collected at the field station. Absolute minimum and maximum temperatures in
99 each month were highly correlated with monthly mean temperatures (Pearson's r
100 = 0.784 and 0.868 respectively), and were therefore not considered separately in
101 our analyses.

102 We quantified monthly food availability using estimated abundance of annual
103 succulents and ephemerals eaten by striped mice (34 species, Schradin (2006)).
104 These plants vary seasonally in abundance and are the main driver of both changes
105 in metabolic rates (Rimbach *et al.*, 2018) and reproduction (Nel *et al.*, 2015) of
106 striped mice. We estimated plant abundance based on a vegetation survey within

107 the study site. Eight monitoring plots (2 x 2 m each) were sampled monthly using
108 a standard protocol (Braun-Blanquet method, Werger (1974)) to determine the
109 amount of ground covered by different species of annual succulents and ephemerals.
110 Monthly food availability was then calculated as the plot-average percentage of
111 ground covered by all plant species. We left out the shrub components of striped
112 mouse diet, *Lycium cinereum* and *Zygophyllum retrofractum*, as the former has
113 annual leaves that covary seasonally with the abundance of annual succulents
114 and ephemerals, while the latter is a succulent that varies little within years and
115 represents an "emergency food" for striped mice when nothing else is available
116 (Schradin, 2006). We also did not consider rainfall directly as a covariate as studies
117 have shown that water is not a limiting resource for striped mice (likely due to being
118 available year-round in succulent shrubs, Schoepf *et al.* (2017)), and precipitation
119 thus affects them primarily through the availability of annual food plants.

120 Density regulation is a key component in population dynamics of small mam-
121 mals (Krebs, 2013), and we calculated a proxy for monthly population density by
122 dividing the number of trapped mice by the study area size. We only included
123 adult female mice in the measure, as immature individuals do not compete sig-
124 nificantly for reproduction or food. Males were excluded to allow implementing
125 density feedback in the population model without having to make assumptions
126 about sex ratio in family groups and number of male floaters. Further, competi-
127 tion within sexes can be much more important than between sexes (Wauters *et al.*,
128 2004). This modelling decision was unproblematic as vital rate model selection and
129 matrix model predictions were not sensitive to inclusion of the males in the density
130 measure (results not shown). As a measure for population density was required as
131 a covariate for the mark-recapture model, it was not possible to correct the counts

132 of trapped mice with recapture probabilities at that stage. However, due to overall
133 high and invariable recapture probabilities over the study period, the raw counts
134 are representative of the total population size (Nater *et al.*, 2016a). The size of
135 the study site varied throughout the study period due to changes in the size of
136 individual home ranges (Schradin *et al.*, 2010), and we estimated it using a 100%
137 minimum convex polygon (MCP) approach (Worton, 1987) on the coordinates of
138 the sampled nests in each month.

139 **ADAPTATION OF VITAL RATE ESTIMATION**

140 In a previous study (Nater *et al.*, 2016a) we had estimated several monthly vital
141 rates of female striped mice as functions of ambient temperature, food availability,
142 and population density for the period from January 2005 to September 2014.
143 Specifically, we had used (1) a multi-state mark recapture model (Lebreton *et al.*,
144 2009) to estimate monthly survival and maturation probabilities of immatures
145 (S_i, Ψ_{ib}) and philopatrics (S_p, Ψ_{pb}), and survival probability of breeders (S_b), (2) a
146 generalized linear mixed model (GLMM) to estimate the breeding probability (B)
147 of breeders and (3) GLMs to estimate litter probability (L) and litter size (F). For
148 using the vital rate - environment relationships in a matrix population model in
149 this study, we re-defined the breeder stage to accommodate a pure post-breeding
150 census and elevated litter size using auxiliary data to obtain population projections
151 that did not go extinct within a few months. These adaptations and the resulting
152 re-analyses of vital rate - environment relationships are detailed in Appendix 1.

153 **STAGE-STRUCTURED POPULATION MODEL**

We used the re-estimated vital rate - environment relationships to build a stage-structured population model for the female segment of the striped mouse population. We defined population structure at time t ($N(t)$) as a vector containing the number of immatures ($N_i(t)$), philopatrics ($N_p(t)$) and breeders ($N_b(t)$):

$$N(t) = \begin{bmatrix} N_i(t) \\ N_p(t) \\ N_b(t) \end{bmatrix}$$

We then defined transition matrices $A(t)$ (for more information see Caswell, 2001) that describe the monthly transitions between these stages depending on the vital rates in striped mouse life cycle (Figure 1). As all vital rates were functions of monthly temperature, food availability, and population density, the matrix itself was dependent on these environmental covariates (indicated by time-dependence of A):

$$A(t) = \begin{bmatrix} S_i\Psi_{ib}LF & S_p\Psi_{pb}LF & S_bBLF \\ S_i(1 - \Psi_{ib}) & S_p(1 - \Psi_{pb}) & 0 \\ S_i\Psi_{ib} & S_p\Psi_{pb} & S_b \end{bmatrix}$$

154

155 This allowed projecting population size and structure from a given month t to the
156 next ($t + 1$) using $N(t + 1) = A(t)N(t)$.

157

158 We assessed the ability of the matrix model to capture striped mouse popula-
159 tion dynamics by comparing model-generated population hindcasts to the observed

160 population sizes over the course of the study period. We used the observed num-
161 bers of immatures, philopatrics and breeders at the beginning of the time series to
162 define the initial population vectors $N(t = 1)$ and $N(t = 2)$. We then projected the
163 population for 116 time steps using projection matrices $A(t)$ generated with the
164 observed time-series of temperature and food availability. The density covariate
165 was calculated from the projected population size $N(t)$ at every timestep (details
166 in Appendix 2), thus letting population density propagate within the model. We
167 ran one projection using the specific year random effect values estimated by the
168 breeding probability model and another 100 trajectories by sampling this random
169 effect from a normal distribution with the estimated variance. Subsequently, we
170 compared the monthly population numbers predicted by matrix model projections
171 to the observed number of trapped mice in each month.

172 **RANDOM DESIGN LTRE**

173 Population dynamics show responses of varying magnitude to changes in differ-
174 ent vital rates and the environmental drivers underlying these changes (Oli, 2004;
175 Coulson *et al.*, 2000). Life Table Response Experiments (LTREs) are retrospective
176 perturbation tools for quantifying relative impacts of matrix elements, vital rates
177 and lower-level covariates on previously observed population dynamics (Caswell,
178 2001). The dominant right eigenvalues of the matrices (λ) is often used as the re-
179 sponse variable of interest in LTREs as it represents long-term population growth
180 rate for density-independent populations in constant environments (Caswell, 2001).
181 Despite this definition not applying here, λ was highly correlated with transient,
182 one-time-step growth rate in our model (Appendix 4: Figures S4.1 & S4.2), and
183 we thus used it as the response variable of an LTRE analysis (for results using

184 transient one-time-step growth rate instead, see Appendix 3). As we had 116 dif-
185 ferent matrices available (one for each month of the study period), we used a
186 random design LTRE (Caswell, 2001, chapter 10.2) to decompose temporal vari-
187 ation in λ into contributions from variation in all different vital rates and from
188 the changes in temperature, food availability and population density underlying
189 it. This required sensitivity estimates of λ to changes in environmental covariates,
190 vital rates and matrix elements, and we calculated these numerically using the
191 element-by-element mean of all 116 matrices as a reference (Horvitz *et al.*, 1997).
192 We performed the random design LTRE analysis for all matrices together, as well
193 as pooled into three seasons: breeding season (Aug - Nov), dry season (Dec - Mar)
194 and cold season (Apr - Jul).

195 **QUALITATIVE HINDCAST PERTURBATION**

196 Projections from our matrix model were characterized by population peaks of
197 varying frequency and amplitude (Figure 2). To gain insight into the roles of envi-
198 ronmental covariates in producing these patterns in our model, we did a qualitative
199 hindcast perturbation analysis. Specifically, we created 6 hindcast projections in
200 which we disabled the effects of one or two of the environmental drivers by set-
201 ting them to a constant value, and compared these projections to the unperturbed
202 hindcast. The constant value chosen for all covariates was their mean over the
203 study period, and the random year effect on breeding probability was set to 0
204 here.

205 **STOCHASTIC DYNAMICS IN A STATIONARY ENVIRONMENT**

206 Stochasticity in environmental conditions is ubiquitous and can strongly influence
207 the dynamics of populations (Tuljapurkar, 2013), particularly in combination with
208 with density-dependence (Boyce *et al.*, 2006; Sæther, 1997). Understanding pop-
209 ulation dynamics of species like striped mice that inhabit a variable environment
210 and are strongly density-regulated thus requires consideration of environmental
211 stochasticity. We analyzed population dynamics in a stochastic but stationary en-
212 vironment with a prospective perturbation analysis. We generated 10,000 stochas-
213 tic 200-year time series of temperature and food availability by randomly sampling
214 sequences of the covariates from all years we had data for (2005 - 2014). We defined
215 the year as starting in April, as the population is generally between maximum and
216 minimum densities in this month and each year then contains a distinctive popula-
217 tion peak and trough. For each replicate time-series, we then created two perturbed
218 scenarios in which either temperature (S_T) or food availability (S_F) was increased
219 by 1%. We used unperturbed and perturbed environment time-series to simulate
220 future population trajectories, starting the projections using observed population
221 numbers and stage distributions for April 2005. For the stochastic projections, we
222 introduced a maximum litter size threshold of 5.8 (maximum value in the data)
223 to prevent unrealistic behavior of the exponential litter size model.

224 For each population projection we obtained this way, we determined population
225 size and structure during the population maximum and minimum in each year.
226 Subsequently we calculated the fold-changes of population size and structure, as
227 well as quasi-extinction probability (threshold = 5 females), in scenarios S_T and
228 S_F relative to the unperturbed scenario. Finally, we used additional simulations

229 in a pathway analysis to determine which vital rates were primarily responsible
230 for the calculated changes in annual minimum/maximum population sizes under
231 scenarios S_T and S_F . We describe this analysis in more detail in Appendix 2.

232 STOCHASTIC DYNAMICS IN A CHANGING ENVIRONMENT

233 When studying population responses to climate change, a gradual instead of a
234 constant change in temperature (and potentially other environmental factors) has
235 to be considered (Wolkovich *et al.*, 2014). We explored how stochastic population
236 dynamics of striped mice changed when the population experienced a gradual in-
237 crease in temperature. The magnitude of this temperature change was inspired
238 by climate change scenarios for South Africa. General Circulation Models predict
239 climate warming in the Succulent Karoo to range from 0.01°C to 0.4°C per year
240 until the end of the century, with the majority of models predicting an increase
241 of 0.02°C to 0.03°C per year (Jury, 2013). We thus assumed an annual tempera-
242 ture increase of 0.025°C for our first climate change scenario ($S_{T\uparrow}$). It is unlikely
243 that the availability of food plants for striped mice will remain unchanged in the
244 future, as rainfall is generally expected to decrease. Climate change scenarios for
245 rainfall in South Africa are very variable and subject to large local differences
246 (MacKellar *et al.*, 2007; Collier *et al.*, 2008), however. This, in combination with
247 direct detrimental effects of increasing temperatures on Karoo vegetation (Musil
248 *et al.*, 2009), makes quantitative predictions of vegetation changes very difficult.
249 We therefore adopted an exploratory approach regarding changes in food availabil-
250 ity and included two additional climate change scenarios in which food availability
251 was expected to gradually decrease up to 10% ($S_{T\uparrow F\downarrow}$) or 20% ($S_{T\uparrow F\downarrow\downarrow}$) within 100
252 years.

253 For each climate change scenario, we generated 20,000 100-year stochastic en-
254 vironment time series and perturbed them by imposing trends in temperature
255 and food availability as described above. We then ran population projections for
256 1200 time-steps using the original and perturbed environment time series, and an-
257 alyzed changes in annual minimum/maximum population sizes and population
258 structures. Contrary to the analyses on stationary environments, we here not
259 only looked at the correlation between the original and perturbed trajectories,
260 but also accounted for temporal changes by fitting a linear model of the form
261 $X_{perturbed} \sim X_{original} + year + year : X_{original}$ where X represents the quantity of
262 interest (population size or structure). For each simulation in each scenario, we
263 used the parameters of this linear model to make an estimate of the fold-change
264 in X after 100 years of exposure to the climate change scenario. The "original"
265 population size and structure we used in those calculations were based on the
266 mean value for the entire unperturbed scenario for each simulation. In a last step,
267 we quantified the contributions of different demographic pathways to changes in
268 annual minimum/maximum population sizes after 100 year exposure to climate
269 change scenarios (details in Appendix 2).
270 All matrix model analyses were done in R version 3.4.0 (R Core Team, 2015).

271 Results

272 MODEL FIT & POPULATION GROWTH RATES

273 A model hindcast using the observed levels for the random effects in breeding prob-
274 ability performed well at capturing observed population dynamics (Figure 2). The
275 timing of population increases and decreases was well represented by the model,

276 but peak population sizes tended to be somewhat overestimated. Furthermore, we
277 demonstrated that even when the values of the random year effects on breeding
278 probabilities were sampled randomly, the predicted pattern was well preserved.

279 We calculated two measures of population growth rate for each of the 116 ma-
280 trices. The dominant right eigenvalues of the time-specific matrices ranged from
281 0.82 to 1.6 (mean = 1.01, SD = 0.18). Transient one-time-step growth rates (calcu-
282 lated using both time-specific matrices and observed population structures) took
283 values between 0.81 and 1.95 (mean = 1.06, SD = 0.25). Dominant right eigenval-
284 ues and transient growth rate followed the same pattern and were numerically very
285 similar (Appendix 4: Figure S4.1). 93% of variation in transient growth rates was
286 explained by the dominant right eigenvalues of the matrices (Appendix 4: Figure
287 S4.2).

288 **RELATIVE STRENGTHS OF DRIVERS OF PAST POPULATION** 289 **CHANGE**

290 Decomposition of variation in the dominant right eigenvalues of the matrices using
291 a random design LTRE identified food availability, working primarily through lit-
292 ter size, as the main driver of past population changes. The contribution of changes
293 in food availability was 0.021, and thus three times as large as the next influential
294 quantity, variation in population density (contribution = 0.007). Contributions
295 from variation in temperature and covariation among different environmental fac-
296 tors were comparatively small (Figure 3). Among vital rates, the strongest contri-
297 bution came from variation in litter size (0.008), followed by variation in philopatric
298 maturation probability (0.005, Appendix 4: Figure S4.4). Other considerable con-
299 tributions came from variation in breeding probability and litter probability, as

300 well as their covariances with each other and with philopatric maturation proba-
301 bility. These relative rankings were conserved when variation in transient growth
302 rate (instead of dominant right eigenvalue) was the quantity of interest (Appendix
303 3).

304 Seasonal analysis revealed that food availability only had the largest contribu-
305 tions in the breeding and the cold season. In the dry season, the largest contri-
306 bution was ascribed to population density (Appendix 4, Figure S4.3). Similarly,
307 contributions from philopatric maturation probability were more important than
308 contributions from litter size in the dry season only (Appendix 4, Figure S4.5).

309 **QUALITATIVE PERTURBATION OF POPULATION HINDCASTS**

310 Excluding temporal variation in environmental covariates led to different changes
311 in population dynamics (Figure 4). Removing temperature variation resulted in
312 only slight changes in the height of population peaks. When the effect of food
313 availability was ignored, on the other hand, both population increases and de-
314 creases were lost almost completely, irrespective of whether or not temperature
315 was allowed to vary. Finally, disabling the density feedback led to rapid population
316 explosion. Again, this was the case both with varying and constant temperature.
317 Disabling the density feedback in the presence of constant food availability re-
318 sulted in a population that was almost constant at a small size, and showed only
319 low amplitude fluctuations as a consequence of varying temperature.

320 **STOCHASTIC DYNAMICS**

321 Population trajectories obtained for stochastic environments were characterized
322 by marked differences in peak population sizes (Appendix 4: Figure S4.6), but

323 every peak was followed by a similar crash. This behavior led to perturbed trajec-
324 tories that differed from original trajectories in minimum and maximum annual
325 population sizes, but did not diverge strongly from original trajectories over time
326 (Appendix 4: Figure S4.7).

327 Population peaks in stationary environments became higher when either tem-
328 perature (mean fold-change = 1.009) or food availability (mean fold-change =
329 1.025) was increased by 1% (Figure 5a & b). In both perturbations, these increases
330 were primarily driven by changes in litter size and the maturation probability of
331 immatures (Figure 5c & d). Minimum population sizes became larger under in-
332 creased food availability (mean corr. coefficient = 1.005) due to changes in litter
333 probability, breeding probability and philopatric maturation probability. Increased
334 temperature, on the other hand, could lead to either smaller or larger minimum
335 population sizes depending on the stochastic sequence of years, and contributions
336 were spread over several vital rates (Figure 5b & d). Perturbations also affected
337 population structure: during population peaks and lows, higher temperature led to
338 a larger proportion of philopatrics, while higher food availability resulted in more
339 philopatrics and breeders (Appendix 4: Table S4.1). Extinction probability over
340 the simulated 200-year period was small at 5.2% for unperturbed trajectories, but
341 decreased further to 4.8% and 4.9% when temperature and food availability were
342 increased.

343 Annual maximum and minimum population sizes displayed distinct responses
344 to different climate change scenarios (Figure 6a & b). With gradually increas-
345 ing temperature but no change in food availability ($S_{T\uparrow}$), peak population sizes
346 increased by 11.2%, while minimum population sizes decreased by 2.6% on av-
347 erage over a 100-year period. This positive effect of increasing temperature on

348 peak population sizes was offset if accompanied by a 10 % gradual decrease in
349 food availability ($S_{T\uparrow F\downarrow}$): Maximum population size after 100 years was lower in
350 all simulations, with an average decrease of 10.1%. Minimum population size de-
351 creased by an average of 4.2%, although increases were seen in some simulations
352 (Figure 6b). When food availability decreased even more (20% in $S_{T\uparrow F\downarrow\downarrow}$), maxi-
353 mum population size decreased by 29.6% and minimum population size by 12.7%
354 on average. Decreases in minimum population sizes were driven by changes in mat-
355 uration, breeding and litter probabilities. The same vital rates were responsible for
356 lower peak population sizes under $S_{T\uparrow F\downarrow}$ and $S_{T\uparrow F\downarrow\downarrow}$, while the higher population
357 peaks under $S_{T\uparrow}$) were primarily due to changes in litter size.

358 Stage structure during the maximum and minimum population sizes was af-
359 fected similarly by all three climate changes scenarios: Populations had a consid-
360 erably higher proportion of philopatrics and lower proportion of breeders after 100
361 years of exposure to the scenarios (Appendix 4: Figure S4.8 & Table S4.2). The
362 proportion of immatures on the other hand decreased only when food availability
363 was projected to go down ($S_{T\uparrow F\downarrow}$ & $S_{T\uparrow F\downarrow\downarrow}$) and showed very variable responses
364 when only temperature increased ($S_{T\uparrow}$).

365 Extinction probability was almost halved when temperature increased gradu-
366 ally (decrease from 2.6% without perturbation to 1.4% under $S_{T\uparrow}$, fold decrease =
367 1.83). An accompanying moderate decrease in food availability ($S_{T\uparrow F\downarrow}$) resulted in
368 a 1.29-fold decrease in extinction probability (2.6 to 2.0%), whereas with a higher
369 food decrease ($S_{T\uparrow F\downarrow\downarrow}$), it increased 1.45-fold (2.6 to 3.8%).

370

371 Discussion

372 In this study, we analysed population dynamics of a small semi-desert rodent
373 on multiple temporal scales ranging from short-term month-by-month changes to
374 long-term projections spanning several decades. By explicitly including environment-
375 demography relationships, we obtained a population model able to reproduce past
376 population dynamics and identified food availability affecting reproduction and re-
377 sulting density feedbacks as the main mechanisms driving the strongly fluctuating
378 population dynamics of our study species.

379 Analysing the population dynamics on short timescales, we found that variation
380 in monthly population growth rates was mainly due to changes in food availability
381 (Figure 3) affecting vital rates linked to reproduction (predominantly litter size,
382 Appendix 4: Figure S4.4). The same general pattern emerged for multi-annual
383 stochastic population dynamics: elevating food availability resulted in larger pop-
384 ulation sizes during annual peak and low phases as a result of changes in matura-
385 tion rates and reproductive output (Figure 5). The importance of food availability
386 was emphasized further by the fact that population fluctuations largely disap-
387 peared when variation in plant cover was ignored (Figure 4). These findings are
388 consistent with other studies that found food availability to be the main driver
389 of population fluctuations of rodents in semi-arid environments (Brown & Ernest,
390 2002; Previtali *et al.*, 2010; Lima *et al.*, 2008), as well as primary consumers in
391 general (Hunter & Price, 1992; Kagata & Ohgushi, 2006). In the case of striped
392 mice, opportunistic breeders displaying a high degree of plasticity in reproductive
393 timing (Raynaud & Schradin, 2008; Nel *et al.*, 2015), the population increases fol-
394 lowing elevated food availability are likely the results of prolonged reproductive

395 seasons with many young animals starting to breed early, potentially followed by
396 "out-of-season" reproduction due to more favorable conditions.

397 The second-most important driver of changes in monthly population growth
398 rates was population density (Figure 3). Variation in population growth rates dur-
399 ing months with scarce food (dry season) was even primarily due to changes in
400 population density (Appendix 4: Figure S4.3). Stronger density feedbacks when
401 populations are close to their carrying capacity (*e.g.* due to resource scarcity) have
402 been found in a range of species including other rodents (Goswami *et al.*, 2011), un-
403 gulates (Albon *et al.*, 2000; Coulson *et al.*, 2001), and raptors (Krüger, 2007). This
404 reflects the importance of population density in regulating and stabilizing popu-
405 lation dynamics (Hanski, 1990), and is further supported by our model predicting
406 either rapid population explosion or extinction when the density feedback was
407 disabled (Figure 4). The impacts of density feedbacks were very evident in multi-
408 annual population dynamics as well: While both increases in food availability or
409 temperature led to larger annual minimum and maximum population sizes (Figure
410 5a & b), these changes did not add up over time and populations in perturbed en-
411 vironments did not progressively diverge from those in unperturbed environments
412 (Appendix 4: Figure 4.7). This indicates that density regulation is strong enough to
413 "reset" population dynamics every year, and supports the hypothesis that strong
414 density feedbacks buffer populations of fast-living species against environmental
415 change (Williams, 2013).

416 Temperature only explained a small fraction ($\approx 4\%$) of the variation in short-
417 term population growth rates (Figures 3) and increasing it led to smaller changes
418 in long-term population abundances than increasing food availability (Figures 5).
419 This is a result of relatively weaker impacts of temperature on vital rates (Nater

420 *et al.*, 2016a), and may be partially related to the generally lower interannual
421 variation in temperature relative to food availability and population density.

422 Long-term population responses of striped mice under climate change scenarios
423 depended strongly on the assumed change in food availability. Rising temperatures
424 alone resulted in larger annual population peaks as a consequence of increased lit-
425 ter size (particularly outside the main breeding season), and variable responses of
426 annual minimum population size (Figure 6). Adding a gradual decrease in food
427 availability, however, led to reduced maturation, breeding and litter probabilities,
428 and ultimately populations with overall lower abundance (minimum and maxi-
429 mum population sizes, Figure 6). The strength of this response scaled with the
430 magnitude of the food decline. This lower reproductive output during the main
431 breeding season led to lower peak densities, which in turn let more philopatrics sur-
432 vive the dry season and thus contribute to the following minimum population size.
433 This is supported by the generally higher percentage of philopatrics in populations
434 experiencing climate change (Appendix 4: Figure S4.8). Striped mice are known
435 to delay reproduction, likely to increase their chances of surviving the harsh dry
436 season and then breed the following spring (Schradin *et al.*, 2012). Our analyses
437 indicate that under harsher conditions (*e.g.* increasing temperatures and decreas-
438 ing food availability associated with climate change), more mice may be forced
439 to adopt this strategy, and possibly for a longer period of time. Delayed maturity
440 under adverse environmental conditions has been studied in long-lived species (*e.g.*
441 seabirds, Nevoux *et al.* (2010)), but less in short-lived species, making the striped
442 mouse an interesting system for future study of the role of delayed reproduction
443 in mediating environmental change.

444 The quasi-extinction probability of striped mouse populations over 100 years

445 increased only under the scenario with the strong decrease in food availability
446 ($S_{T\uparrow F\downarrow\downarrow}$), and even then was still quite low at 3.8%. This too is related to the strong
447 density feedback stabilizing the population and thus buffering it even against large
448 changes in the environment. Under the investigated scenarios, our simulations thus
449 do not indicate that gradual climate change threatens persistence of striped mice
450 in the Succulent Karoo. However, the climate change scenarios we used here may
451 be only partially representative of future environmental change, and future studies
452 could improve on this from two perspectives.

453 First, the simulated decreases in vegetation cover were only qualitatively linked
454 to predicted future changes in rainfall and scenarios may therefore not accurately
455 represent the expected change in food availability due to climate change. Hav-
456 ing a model linking vital rates directly to food availability - instead of indirectly
457 through rainfall as done in many other studies on arid ecosystems (*e.g.* Ozgul *et al.*,
458 2014) - granted us more insight into the biological mechanisms underlying popu-
459 lation dynamics. However, the downside of this is that in order to run this model
460 under more realistic climate change scenarios, the relationship between rainfall
461 and vegetation cover needs to be quantified. This is a non-trivial task, as vegeta-
462 tion responds to rainfall in a complex and non-linear way, depending not only on
463 amount but also timing of rainfall (*e.g.* 100mm of rain over the course of a month
464 stimulating plant growth vs. 100mm of rain falling within one day and destroying
465 vegetation). Second, climate change will not only lead to gradual changes in mean
466 environmental variables, but also increases in the frequency of extreme weather
467 events (IPCC, 2014). We have not considered such events in the current study,
468 but they can potentially have strong impacts on population dynamics (van de Pol
469 *et al.*, 2010). In semi-arid Chile, for example, extreme flooding events following

470 catastrophic rainfalls can reset long-term demographic trends and community dy-
471 namics (Kelt, 2011), and similar flooding events can occur in the Succulent Karoo
472 with potentially detrimental consequences for striped mice. Extreme events also
473 happen in the form of droughts and temperature anomalies, such as in the un-
474 usually dry winter of 2003 which wiped out almost our entire study population
475 (pers. observation). So while the results from this study indicate that moderate
476 trends in average temperature and food availability do not threaten viability of
477 striped mouse populations, the same may not be true for changes in frequency and
478 intensity of extreme weather events. Quantifying the general relationship between
479 vegetation cover and rainfall, as well as occurrence and consequences of extreme
480 events (*e.g.* floods, droughts), are thus important topics for future research and will
481 allow us to make more realistic predictions of striped mouse population responses
482 to climate change.

483 Another area to improve on is the accuracy of numerical predictions. While our
484 population model produced a good fit to observed data, achieving this numerical
485 accuracy required adjustment of litter size estimates using auxiliary information.
486 The original measure of litter size had been consistently too low due to a combina-
487 tion of low detectability of immatures and potential overestimation of the number
488 of breeding females (Appendix 1, Section 1.2). In order to obtain more accurate
489 numerical predictions, future studies should aim to quantify litter size more pre-
490 cisely. This could be done, for example, by using open population mark-recapture
491 designs to account for the low detectability of immatures (Pradel, 1996), larger-
492 scale genetic studies (*sensu* Schradin *et al.* (2012)) to reliably identify the females
493 giving birth and their offspring, and experiments investigating the environmental
494 effects on both the actual number of pups born to a female as well as nest survival

495 of those pups.

496 Lastly, and particularly when discussing responses to climate change, one has
497 to keep in mind that in this study, we have considered only a single population
498 of striped mice in isolation, ignoring immigration and spatial dynamics and ac-
499 counting for predation only indirectly (through survival estimates, Nater *et al.*
500 (2016a)). However, interactions and movement between different striped mouse
501 populations are likely important, and so is the general role of striped mice in the
502 foodweb. In (semi-)arid environments, small mammals often have important roles
503 as keystone (prey) species and ecological engineers (Kelt, 2011). If climate change
504 reduced overall abundance of striped mice (and potentially other rodent species) -
505 as predicted in this study - this could have cascading effects on the abundance of
506 bird, reptile, and carnivore predators (Byrom *et al.*, 2014), on the spread of inva-
507 sive species (Madrigal *et al.*, 2011), and on the plant species richness that makes
508 the Succulent Karoo a unique biodiversity hotspot (Hillebrand *et al.*, 2007). Such
509 effects on other trophic levels could, in turn, feed back again on rodent (meta-
510)population dynamics. To make realistic predictions on how the Succulent Karoo
511 as a whole (and similar biomes) will respond to climate change, an ecosystem ap-
512 proach coupling climate to plant, rodent and predator populations and including
513 feedbacks between the different trophic levels will therefore be invaluable.

514

515 Environmental factors and density feedbacks have long been recognized as the
516 key determinants of population dynamics, and studying these relationships via
517 variation in vital rates has emerged as a powerful approach (Gamelon *et al.*, 2017).
518 Nonetheless, environmental factors are rarely included into population models ex-
519 plicitly and few models consider interactions between the extrinsic environment

520 and density feedbacks (Ehrlén *et al.*, 2016). In this study, we have accounted for
521 these complexities by building a density-dependent population model based on
522 estimated environment-vital rate relationships. Using this model, we have shown
523 that both short- and long-term population fluctuations of a semi-desert rodent are
524 sensitive to changes in food availability affecting reproduction, but also strongly
525 mediated by intrinsic feedbacks. Strong density dependence thus buffers this popu-
526 lation against environmental change, and the environmentally explicit population
527 model enabled us to gain unique insights into the demographic mechanisms un-
528 derlying this buffering.

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536 **Author's contributions**

537 CN, KB, CC, CS and AO conceived the ideas and designed methodology. CS
538 collected the data. CN and KB analysed the data and led the writing of the
539 manuscript. All authors contributed critically to the drafts and gave final approval
540 for publication.

541 Data accessibility

542 Data available from the Dryad Digital Repository: [https://doi.org/10.5061/](https://doi.org/10.5061/dryad.c1657.2)
543 [dryad.c1657.2](https://doi.org/10.5061/dryad.c1657.2) (Nater *et al.*, 2016b).

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753 **Supporting information**

754 The following Supporting Information is available for this article online: Appen-
755 dices 1-4.

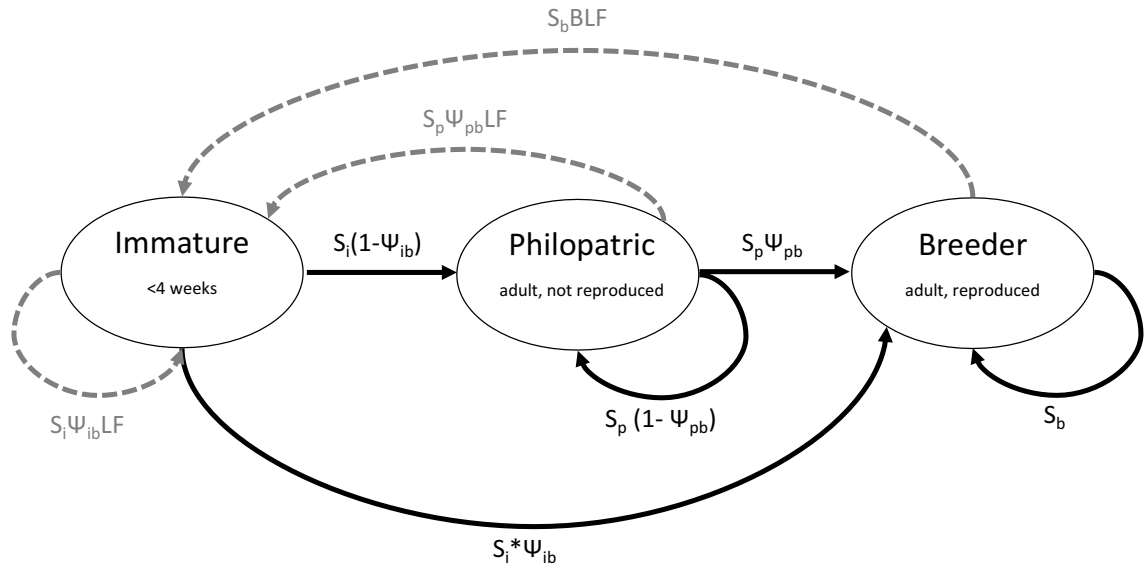


Figure 1: Life cycle of the African striped mouse (post-breeding census). S indicates survival probabilities, Ψ maturation probabilities, B the breeding probability, L the litter probability, and F the litter size. Subscripts for life stages: i = immature, p = philopatric, b = breeder).

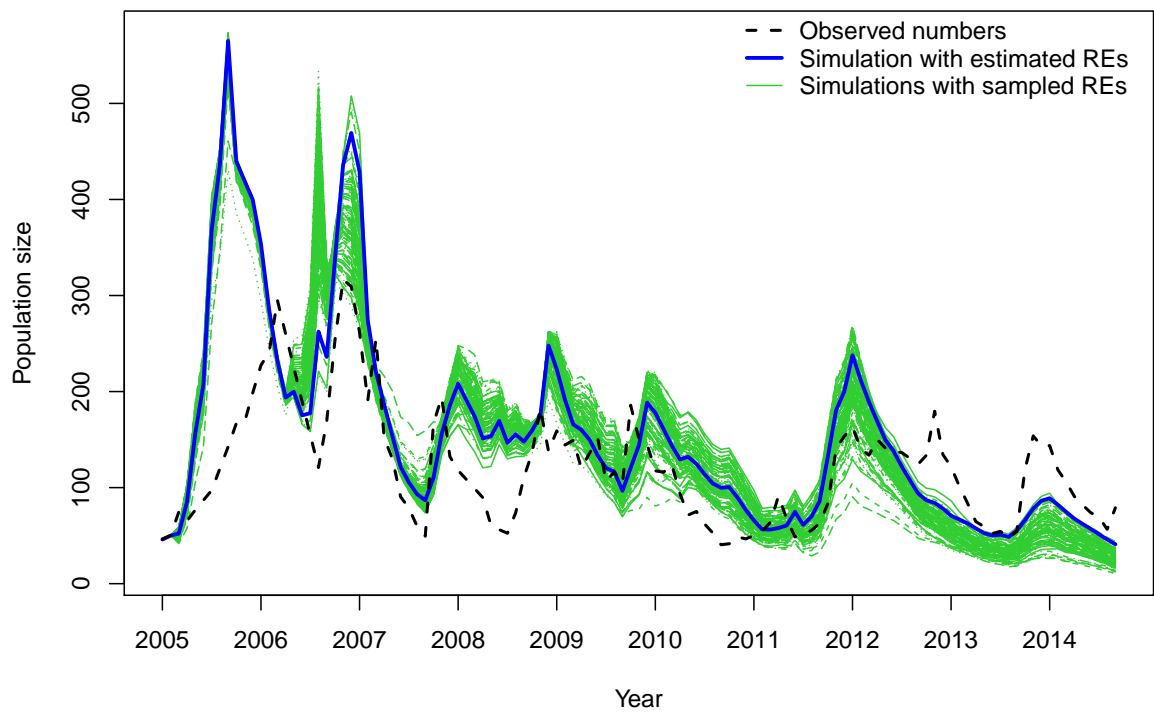


Figure 2: Observed population sizes (black, dashed), model projections using observed levels of random variation (blue), and 100 model projections where random effects were sampled from a normal distribution (green).

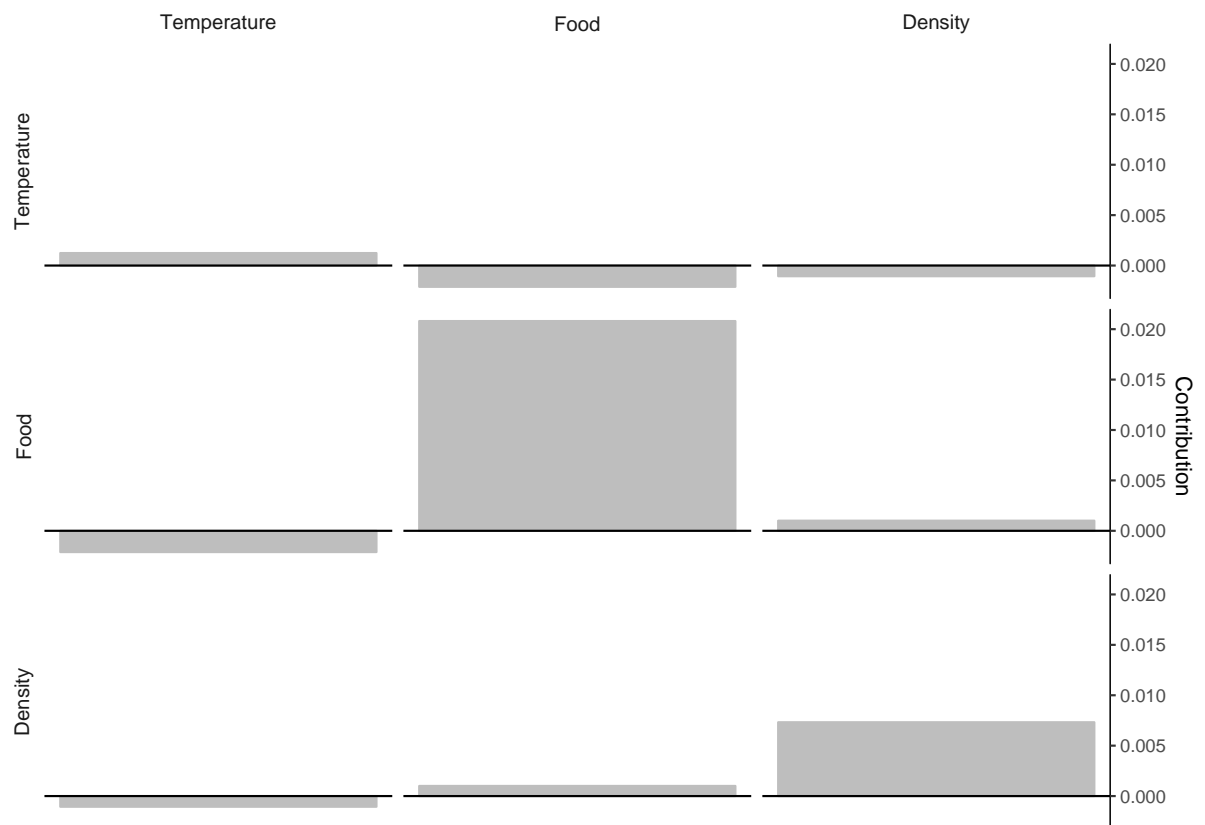


Figure 3: Relative contributions of variances and covariances of temperature, food availability, and population density to variation in the dominant right eigenvalue λ .

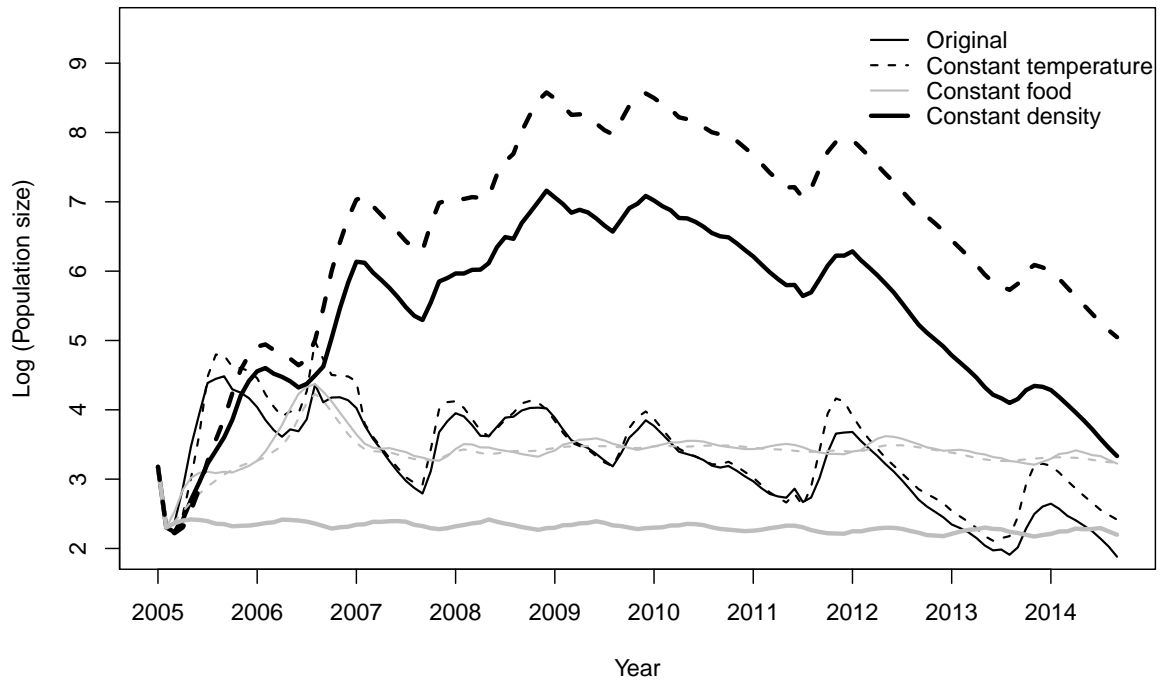


Figure 4: Original and perturbed model hindcasts, where one or two environmental covariates are set to be constant at their mean value. Dashed lines have constant temperature, grey lines have constant food availability, and thick lines have constant density (disabled feedback).

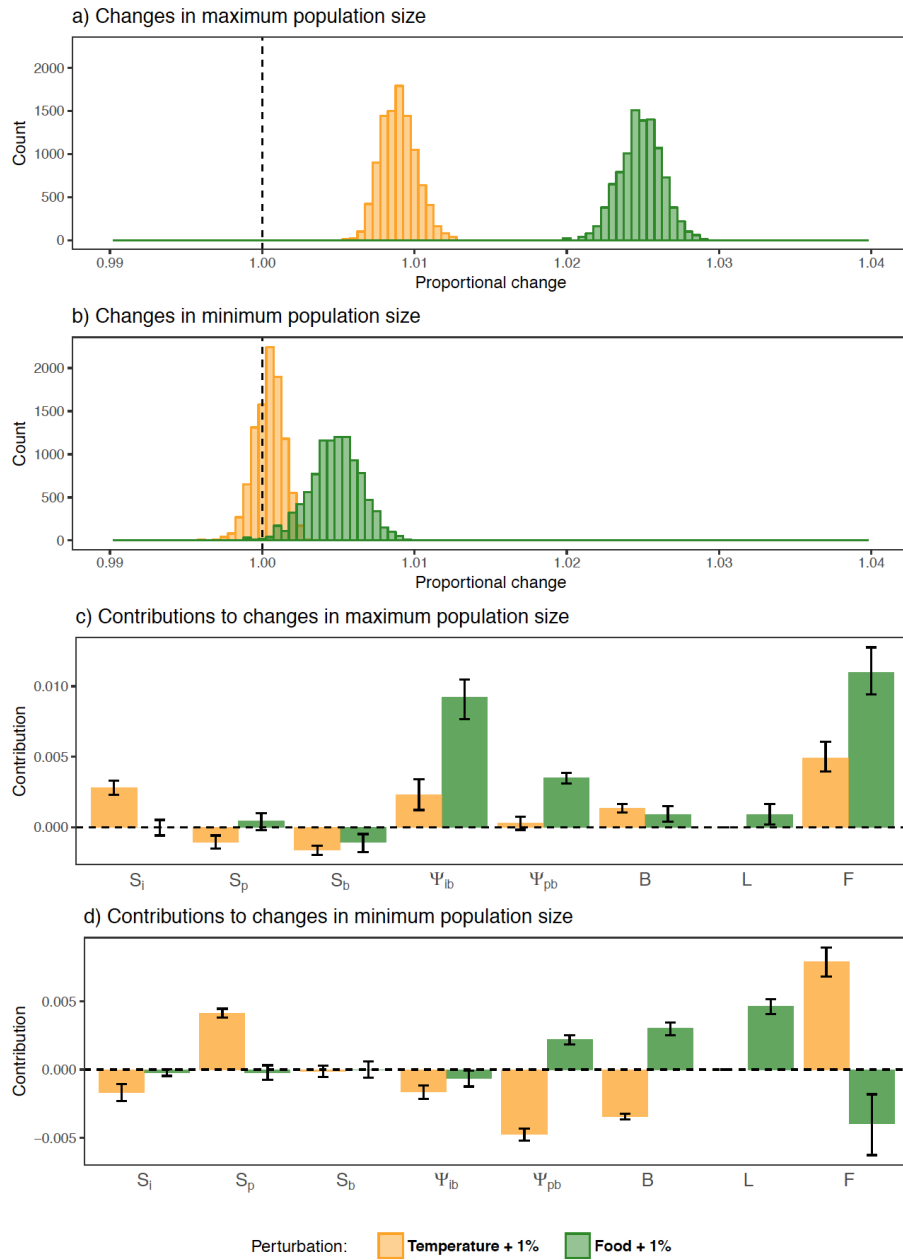


Figure 5: Panels a) and b) show the distributions of proportional change in maximum and minimum population sizes over 200 years when either temperature (orange) or food availability (green) was increased by 1%. Panels c) and d) show the relative contributions of different demographic pathways to those changes. Colored bars represent mean values, black margins mark the 95% confidence interval. Estimates of both population size change and vital rate contributions are based on 10,000 replicates for each scenario.

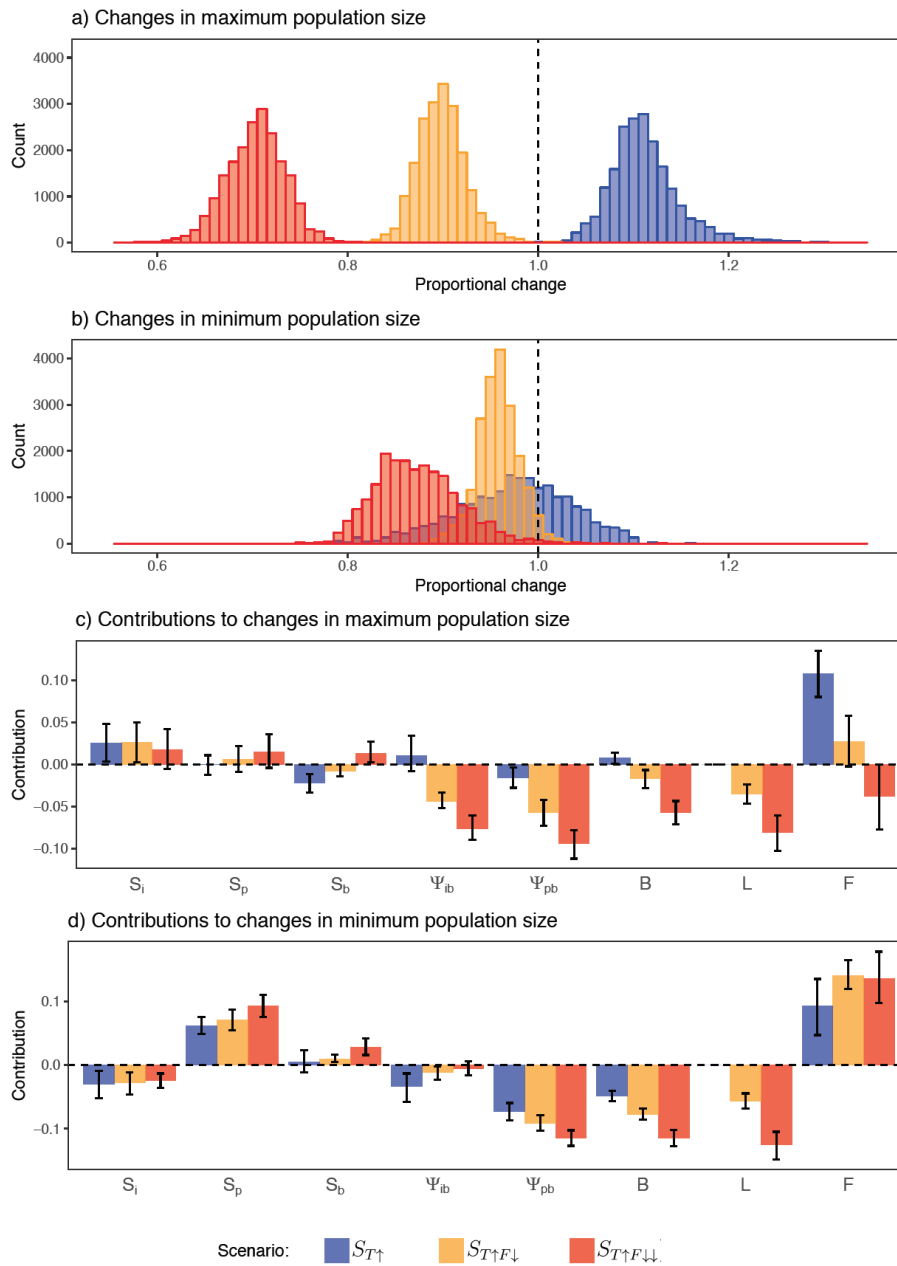


Figure 6: Panels a) and b) show the distributions of proportional change in maximum and minimum population size after a 100-year projection under the three climate change scenarios. Panels c) and d) show the relative contributions of different demographic pathways to those changes. Colored bars represent mean values, black margins mark the 95% confidence interval. Estimates of both population size change and vital rate contributions are based on 20,000 replicates for each scenario.