

1 Evolutionary rescue is determined by differential selection on demographic rates and
2 density dependence.

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5 extinction, demography

6 Accelerated rates of climate change are expected to either lead to populations adapting
7 and persisting, or suffering extinction. Traditionally ecological models make extinction
8 predictions based on how environmental change alters the intrinsic growth rate (r).
9 However, these often ignore potential for evolutionary rescue, or to avoid extinction via
10 adaptive evolution. Moreover, the environment may impose selective pressure on specific
11 demographic rates (birth and death) rather than directly on r (the difference between the
12 birth and death rates). Therefore, when we consider the potential for evolutionary rescue,
13 populations with the same r can have different abilities to persist amidst environmental
14 change. We can't adequately understand evolutionary rescue without accounting for
15 demography, and interactions between density dependence and environmental change.
16 Using stochastic birth-death population models, we found evolutionary rescue more
17 likely when environmental change alters birth rather than the death rate. Furthermore,
18 species that evolve via density dependent selection are less vulnerable to extinction than
19 species that undergo selection independent of population density. Resolving the key
20 demographic factors affected by environmental change can lead to an understanding of
21 how populations evolve to avoid extinction. By incorporating these considerations into
22 our models we can better predict how species will respond to climate change.

23 **Introduction**

24

25 Environmental change can lead to a decrease in population growth rate, resulting in
26 extinction in some cases, and persistence in others. The ability of a population to rebound
27 by attaining a positive growth rate following environmental change is ultimately what
28 allows it to avoid extinction. The need to understand the mechanisms underlying
29 population rebound has spurred studies about demographic rescue (via immigration) and
30 genetic rescue (via an increase in genetic variation) (Brown and Kodric-Brown 1977;
31 Hufbauer et al. 2015; Whiteley et al. 2015). More recently evolutionary rescue, or
32 population rebound due to an increase in density of an adaptive genotype, is a potential
33 mechanism, operating in organisms ranging from microbes (Bell and Gonzalez 2009;
34 Zhang and Buckling 2011) to insects (Agashe et al. 2011) and mammals (Mills et al.
35 2018).

36

37 The search for what makes evolutionary rescue probable has led to an increasing effort to
38 find experimental, empirical and theoretical evidence (Gomulkiewicz and Holt 1995; Orr
39 and Unckless 2008; Bell and Gonzalez 2009, 2011; Johannesson et al. 2011; Gonzalez et
40 al. 2013; Lindsey et al. 2013; Martin et al. 2013; Ramsayer et al. 2013; Mills et al. 2018).

41 Four primary factors affect the propensity for evolutionary rescue (Bell and Gonzalez
42 2009): as initial population size (Ramsayer et al. 2013), genetic variability due to
43 standing genetic variation and mutations (Orr and Unckless 2008), genetic variability due
44 to dispersal (Mills et al. 2018), and the extent and severity of environmental change
45 (Lindsey et al. 2013). Although these results have advanced our understanding of how

46 population growth rate can increase following decline due to environmental change, we
47 still lack a clear understanding of the role of the underlying demographic rates. This is in
48 part because there is wide variation in how environmental change alters population
49 demographic rates (birth and death rates) that is not always explicitly represented in our
50 model frameworks.

51

52 The environment can reduce population growth rate by decreasing the birth rate,
53 increasing the death rate, or some combination of the two (Dempster 1983; McCreddie et
54 al. 1983; Aanes et al. 2000; Sibly et al. 2000, 2005; Clutton-Brock and Coulson 2002;
55 Crump et al. 2004; Brewer and Peltzer 2009). To generalize across taxa, previous studies
56 investigating evolutionary rescue commonly model demographic rates using
57 deterministic models that do not differentiate how the environment acts on the birth and
58 death rates, but rather use a fixed parameter, the intrinsic rate of population increase, r
59 (the difference between the birth rate and the death rate). Consequently, information
60 about changes in a particular demographic rate can be lost if r is the focus of a study.

61

62 Populations with the same r , but different underlying demographic rates, may respond
63 quite differently to environmental selection, affecting how quickly and effectively they
64 adapt (Holt 1990). Take the case of two populations, where one has a high birth and death
65 rate, while another has a low birth and death rate. If the difference between the two rates
66 is equal, both populations will have the same r . But, all else held equal, the population
67 with the higher birth and death rate will have a faster rate of population turnover, and will
68 evolve in response to selection more quickly than the population with the low birth and

69 death rate. A logistic or exponential growth model that depends on a single r value,
70 doesn't allow exploration of how selection and environment affect birth and death rates,
71 and ultimately population extinction or persistence. Therefore, treating birth and death
72 rates explicitly can give insight into which natural populations are more likely to persist
73 via evolutionary rescue in the face of environmental change. So, the potential for
74 successful evolutionary rescue of small populations depends explicitly on birth and death
75 rates, not r , which abstracts away from these rates and obscures the actual speed of
76 adaptation by ignoring the rate of population turnover.

77

78 Density dependence can also affect birth and death rates, and has been shown to influence
79 the dynamics of many species (Sibly et al. 2000; Coulson et al. 2001; Reed and Slade 2008;
80 Ouyang et al. 2014). Environmental change may or may not alter the strength of density
81 dependence; this varies across taxa and type of change (Owen-smith 1990; Sibly et al.
82 2000; Coulson et al. 2001). For example, environmental change leading to a drought may
83 decrease the availability or accessibility of resources (Owen-smith 1990), intensifying
84 density dependence as individuals compete for water-limited resources. Theoretical studies
85 predict that compensatory density dependence, or decrease in growth rate at high densities
86 and increase at low densities, would allow for a larger population size following
87 environmental change (Holt 1990; Ferguson and Ponciano 2015), further facilitating
88 adaptation to new environments. Therefore, establishing the interaction between density
89 dependence and environmental change in different demographic rates is of the utmost
90 importance as the population size following an environmental perturbation determines the
91 probability of extinction.

92 In the past, determining how the environment alters demographic rates in a way that is
93 the most mathematically simple has been sufficient, but, we argue is no longer sufficient
94 when our interest turns to persistence via evolutionary rescue. Therefore, initial studies of
95 evolutionary rescue focusing on r for simplicity, need to be expanded because: (i) they
96 underlying demographic parameters, and (ii) the interaction between environmental
97 change and density dependence may strongly affect evolution. We investigate how the
98 evolutionary rescue depends in detailed ways on how environmental change affects
99 population demographic rates. Here we incorporate environmental conditions and their
100 effects on density dependence into per-capita rates of birth and death, to elucidate their
101 effect on population dynamics and persistence in a stochastic model. We find that
102 populations where the environment affects their death rate as opposed to their birth rate
103 are the most vulnerable to extinction. Furthermore, when environmental change
104 intensifies density dependence, populations are better able to rebound from small
105 population sizes and undergo evolutionary rescue.

106

107 **Methods**

108 *Model Formulation*

109 We construct a continuous-time individual-based logistic growth model, then consider four
110 ways that environmental change might alter population demographic rates. In all cases, as
111 these are logistic growth models, either the birth or death rate is density dependent. In
112 Cases 1a and 1b, the environment alters the birth rate in a density independent and density
113 dependent manner respectively. In Cases 2a and 2b, the environment alters the death rate
114 similarly, in a density independent, and density dependent way. We pay particular attention

115 to ensuring that the four cases converge on the same outcome when the environment is
116 static, to best isolate the effects of life-history and selection on evolutionary rescue.

117

118 *Logistic growth*

119 All of our model cases are rooted in the logistic growth equation where $g(N)$ is a function
120 describing the density dependence of the per-capita growth rate. Note that $g(N) = r$ in the
121 case of exponential growth, as there is no density dependence. We begin with a general
122 equation for the rate of population growth,

123

124
$$\frac{dN}{dt} = g(N)N \quad (0.1)$$

125 .

126 Since $g(N)$ is equal to the difference between the per capita birth rate b and the per capita
127 death rate d , we can rewrite equation (0.1) as the difference between birth and death rate,

128

129
$$\frac{dN}{Ndt} = b(\gamma_0, \gamma_1) - d(\gamma_0, \gamma_1) \quad (0.2)$$

130

131 given that both birth and death are governed by density-independent γ_0 , and density-
132 dependent γ_1 contributions. Consistent with most derivations of logistic growth (Nåsell
133 1996, 2001), we assume that density-dependent factors tend to reduce birth rates and
134 increase death rates, leading to the following general definition for birth and death rate
135 functions:

136
$$b(\gamma_0, \gamma_1) = b_0 - \gamma_0 - \gamma_1 \left(\frac{b_0 - d_0}{K_A} \right) \quad (0.3)$$

137

138
$$d(\gamma_0, \gamma_1) = d_0 + \gamma_0 + \gamma_1 \left(\frac{b_0 - d_0}{K_A} \right) \quad (0.4)$$

139

140 Where b_0, d_0 represents a modification of the background density-independent birth and
141 death rates and K_A is the maximum carrying capacity.

142

143 *Environmental effect*

144 We allow different demographic rates to depend on the environment and traits of
145 individuals. For simplicity and tractability we model the environment μ_0 as a simple
146 sinusoidal function of time (see discussion for our reasons for this choice)

147

148
$$\mu_0(t, f) = \cos(2\pi ft) \quad (0.5)$$

149

150 where f is frequency. We allow individuals to exhibit varied responses to the environment
151 depending on their trait value μ . The effect of the environment, modulated by the trait, is
152 given by

153
$$\varepsilon_\mu = |\mu - \mu_0(t, f)| \quad (0.6)$$

154

155 where a large ε_μ represents a maladapted individual, and a small ε_μ represents a well-
156 adapted individual. We systematically incorporate the environmental effect ε_μ into the
157 density independent γ_0 and density dependent γ_1 components of the birth
158 and death rates. However, to facilitate comparison among the model cases, we scale our
159 equations so that for any value of ε_μ , the equilibrium population size (assuming no
160 temporal environmental change) is the same across all of the model cases. This allows us
161 to make an exact comparison of the impact of temporal environmental change on
162 population dynamics, mediated by ecology and evolution. We do this by assuming that K_A
163 represents the carrying capacity when an entire population is perfectly-adapted to their
164 environment ($\varepsilon_\mu = 0$) and we introduce a second carrying capacity, K_B for a population
165 that is maladapted to their environment ($\varepsilon_\mu = 2$). We then independently solve the
166 parameters γ_0 and γ_1 given the conditions for carrying capacity. When the environment
167 enters via a density-independent route (Cases 1a, 2a), we find:

168

169
$$\gamma_0 = \frac{K_B - K_A}{2K_A} \varepsilon_\mu \quad (0.7)$$

170

171 and γ_1 for the models where the density dependence is altered by environmental change
172 (Cases 1b, 2b)

173
$$\gamma_1 = \left(1 + \frac{K_B - K_A}{2} \varepsilon_\mu \right)^{-1} \quad (0.8)$$

174

175 *Cases 1a-1b, dynamic birth models*

176 We begin with Case 1a, where the environment alters $b(\gamma_0, \gamma_1)$ in a density independent
 177 way as shown in Figure 1a. For case 1b, the environment again alters $b(\gamma_0, \gamma_1)$ but in this
 178 case, it alters population response to density as shown in Figure 1b. For both dynamic birth
 179 models we hold $d(\gamma_0, \gamma_1)$ constant and equal to d_0 .

180

181 *Case 2a-2b, dynamic death models*

182 In Case 2a we now incorporate the environmental effect into $d(\gamma_0, \gamma_1)$ in a density
 183 independent way as shown in Figure 1c. In Case 2b, as in Case 2a, the environment alters
 184 $d(\gamma_0, \gamma_1)$, but now alters population response to density as shown in Figure 1d. In both
 185 cases holding $b(\gamma_0, \gamma_1)$ constant.

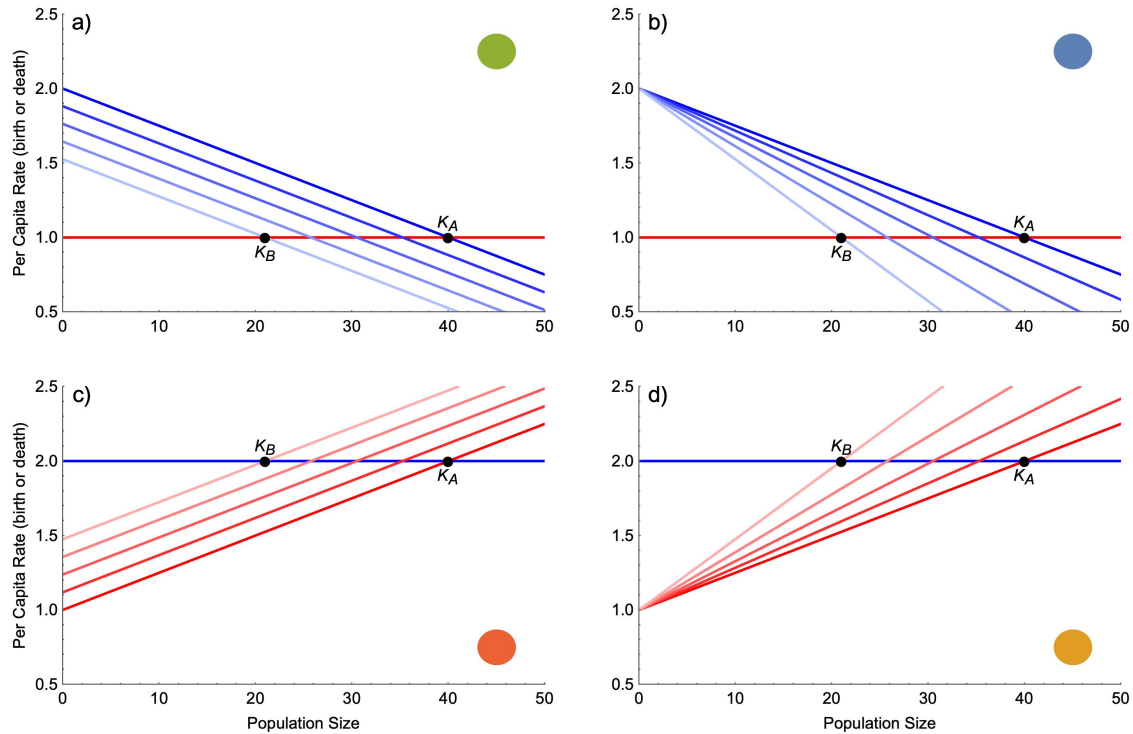
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187 This yields the four model cases described above and laid out in Table 1.

188

Environment enters via:	Density Independent		Density Dependent	
Birth	Case 1a	$b(\gamma_0, N(t))$ $d(0,0)$	Case 1b	$b(0, \gamma_1 N(t))$ $d(0,0)$
Death	Case 2a	$b(0,0)$ $d(\gamma_0, N(t))$	Case 2b	$b(0,0)$ $d(0, \gamma_1 N(t))$

189



190

191 **Figures 1 a-d.** All four cases yield logistic population growth, but depend on different
192 relationships between per-capita demographic rates of birth (blue) and death (red), (see
193 equations 1.3 and 1.4, and table 1). In the upper panels (cases 1a, 1b) death rate is constant,
194 birth rate is density dependent, and the environment either directly increases or decreases
195 birth rate (1a) or changes the strength of the relationship between density and birth rate
196 (i.e., density dependence) (1b). Each blue line depicts the rate of birth for a particular state
197 of adaptation to the environment, ranging from perfectly adapted $\varepsilon_\mu = 0$, as dark blue (top
198 line), to strongly maladapted $\varepsilon_\mu = 2$, as light blue (bottom line). The lower panels show
199 the same relationships for cases 2a and 2b. Colored disks show how the 4 scenarios match
200 to figures 3 and 4.

201

202

203 *Stochastic framework*

204 We used the above ordinary differential equation framework to develop a stochastic
205 simulation algorithm (SSA or birth-death process) using the direct method described by
206 (Gillespie 1977), adapted to allow heritable variation in individual traits. Stochasticity
207 occurs in the model as a result of the random selection of birth and death events
208 (demographic stochasticity), and random mutations during reproduction. This framework
209 is apt for testing our assumptions because true extinctions are possible, and evolution
210 occurs as a result of heritable individual variation that emerges from our assumptions about
211 population demography.

212

213 We initialize the model with 35 individuals with traits drawn from a uniform distribution
214 ranging from -1 to 1, the same range as the possible environmental values. Integration of
215 the model starts by first determining the time until the next event, which is randomly
216 sampled from an exponential distribution with mean $1/E$, where E is the sum of all possible
217 events (birth or death of each individual):

218

219
$$E = \sum_i b(\mu_i) + \sum_i d(\mu_i) \quad (0.9)$$

220

221 After the current time t is updated, the specific event that occurs is determined by randomly
222 choosing among all possible events, weighted according to differences in their rates. For
223 example, the probability that the next event is a death of the i th individual is $d(\mu_i)/E$. If
224 an individual dies, it is removed from the population and the entire process is repeated. If
225 an individual reproduces, a random variable on a uniform (0,1) distribution is chosen. If

226 this value is greater than 0.01, the offspring is assigned the parent's trait value; otherwise,
227 the offspring is given a trait value that is equal to the parent trait value plus a mutation
228 value randomly drawn from a range of -0.3 to 0.3. This sequence of steps mimics mutation-
229 limited evolution in an asexual population. A similar eco-evolutionary framework is
230 described in Delong & Gilbert 2016; however their approach differs slightly from ours
231 because they first aggregate rates of birth and death to the population level, and then
232 randomly assign the individual to experience the event. This results in an underestimate in
233 the response to selection, but leads still to the same equilibrium.

234

235 *Simulations*

236 We conducted simulations across a log-linear range of frequencies (f) of environmental
237 change. For each frequency of environmental change, we conducted 512 independent
238 replicate simulations. We ran the model for 500 time steps before recording the trait values
239 of each individual, as well as the population size and all simulations continued for another
240 10000 time steps or until extinction occurred. Trait-environment correlations were
241 computed for the mean phenotype and environment value using Pearson correlation
242 coefficients. To provide a basis of comparison, we also conducted simulations where
243 mutation driven evolution did not occur.

244

245 Lastly, we conducted simulations utilizing an environment that changes in a logistic
246 manner

$$247 \quad \mu_0(t) = \mu(0)_0 + \frac{\mu(1)_0}{2} \left(1 + \frac{t - T_p}{\sqrt{a + (t - T_p)^2}} \right) \quad (0.10)$$

248 where μ_0 is -1, μ_1 is 1, a is 800 and T_p or the time at which the environment changes is
249 600. The slope of the environmental change is determined by a , which we chose to be a
250 similar slope of change to our sinusoidal environment $f = 0.015$. We used this additional
251 case to showcase a more traditional type of environmental change to observe evolutionary
252 rescue. Simulations were conducted using Wolfram *Mathematica* v11.0 on a iMac Pro with
253 18 Xeon W cores.

254

255 **Results/Discussion**

256

257 Our results show that evolutionary rescue is affected when the environment influences
258 different demographic rates and processes. We begin by discussing the resulting extinction
259 dynamics when considering populations that cannot undergo evolution, followed by
260 populations that have the capacity for mutation driven evolution. The four models we
261 consider here are calibrated to produce the same behavior when the environment is held
262 constant; the population will approach an equilibrium density that is determined by the
263 environment, but is consistent across all cases. At equilibrium, however, the turnover rates
264 (approximated by $\frac{b}{d}$) differ among the models in which birth rates vary amongst
265 individuals and those in which death rates vary (see figure 1). Consistent differences also
266 emerge among the models incorporating the density independent and density dependent
267 environmental interaction; particularly at low densities, the effect of trait variation is
268 strongly buffered in the latter cases. These differences give rise to the results depicted in
269 figure 2.

270 *Demographic results without evolution*

271 The four models exhibit a consistent ranking of mean persistence time across the entire
272 range of frequencies of environmental change we considered. Mean persistence was greater
273 in populations whose birth rates (rather than death rates) were environmentally influenced,
274 and when the environment affected the strength of density dependence. In the absence of
275 evolution, the most persistent populations were of the form outlined in case 1b, followed
276 by case 1a, where there is a density-environment interaction in the birth rate and where the
277 environment acts on the birth rate independent of density respectively. These were
278 followed by case 2b then 2a the populations where the environment altered the strength of
279 density dependence and acted independent of density on the death rate. This ranking in
280 persistence is easily explained by the ecological differences among the models, considering
281 in particular their behavior when population sizes are small (i.e., as populations are near
282 extinction).

283

284 First, populations with birth as the responsive trait persist longer than those with death as
285 the responsive trait due to the greater demographic stochasticity in death models which
286 increases extinction at small pop sizes. The intrinsic growth rate of the population is
287 determined by the difference between the birth and death rate, while demographic
288 stochasticity is determined by the sum of the birth and death rate (Nisbet and Gurney 2003;
289 Palamara et al. 2016). Although our models are parameterized so that they have the same
290 K_A and K_B for when $b - d = 0$, the sum of b and d at these equilibrium points is four
291 times higher in the death models (Case 2a and 2b). Hence the death models have much
292 higher demographic stochasticity than the birth models (Figure 1), and it is clear that

293 demographic stochasticity increases extinction probability at low population sizes (Lande
294 1993; Melbourne and Hastings 2008). Furthermore, demographic stochasticity increases
295 the variance in population size, as we see in figure 2 (a,b). High fluctuations in vital rates
296 has been shown to decrease population growth due to an increase in variation in the
297 population growth rate (May 1973; Jonsson and Wennergren 2019). Accordingly, various
298 species have been shown to be particularly vulnerable to highly variable adult survival,
299 leading to a higher extinction risk (Lande 1988; Caswell et al. 1999; Jonsson and Ebenman
300 2001).

301

302 Secondly, at low densities, models where the environment interacts with the strength of
303 density dependence maintain higher average (and less variable) population size since
304 maladaptation to the environment has a diminishing impact as population size declines (Fig
305 1b, 1d). This is reasonable as populations with highly variable growth rates have been
306 shown to be particularly vulnerable to extinction (Leigh 1981; Lande and Orzack 1988).
307 Furthermore it has been shown with a discrete time model that when the environment is a
308 density dependent term it produces a multiplicative effect on population size, and these
309 populations have more strongly bounded populations (Ferguson and Ponciano 2015). As
310 shown in figure 1 (b and d), at low population sizes the density dependent environmental
311 effect has lower variation than the density independent environmental effect, while the
312 opposite is the case at large population sizes. These differences in variation translate into
313 longer persistence times of the models where environmental change alters the affect of
314 density (case 1b, 2b) relative to those where environmental change alters the vital rates
315 independent of density (case 1a, 2a). Although the environmental density effect increases

316 variation at high population sizes, it is favorable when populations are small as they are
317 better able to rebound.

318

319 All four scenarios exhibit a rising persistence time as the frequency of environmental
320 variation increases. This is driven by a phenomenon known as “ecological tracking”; when
321 a population ecologically tracks its environment, changes in the environment are re-
322 expressed in the population dynamics as correlated changes in density. Here, where the
323 environment changes sinusoidally, ecological tracking generates population dynamics that
324 exhibit a noisy cycle at the same frequency as the environment (figure 3a,c); however, the
325 tracking response of population diminishes as f increases. (May 1976) suggested that the
326 quantity, which represents the system’s dominant eigenvalue, represents a threshold
327 frequency above which tracking does not occur in the Logistic model, but the exact
328 relationship between tracking and the frequency of oscillations is best described as a
329 continuous sigmoid function (Vasseur 2007). The stronger tracking response generated at
330 low frequencies of environmental variation leads to greater variation in population density
331 (both above and below the mean) and thus greater extinction risk. This effect has been
332 shown for a variety of ecological scenarios (Heino et al. 2000; Schwager et al. 2006).

333

334 *Demographic results with evolution*

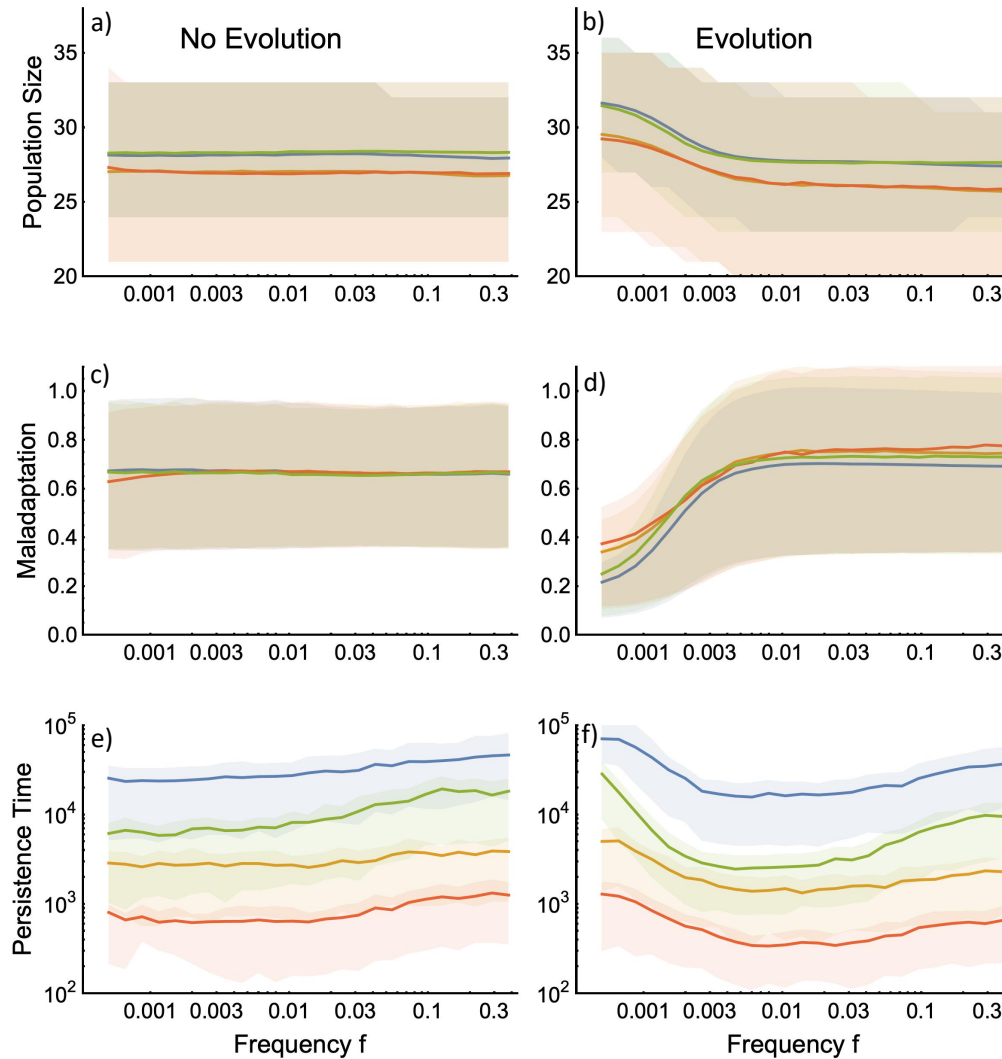
335 When the full eco-evolutionary dynamics are present in our models, we find that the
336 persistence ranking of models is maintained, however all four models demonstrate a U-
337 shaped (rather than monotonic) relationship between the frequency of environmental
338 change and mean persistence times. This U-shaped relationship arises due to the interplay

339 between ecological and evolutionary tracking of the changing environment. Evolutionary
340 tracking occurs when changes in the environment are slow enough that they can be re-
341 expressed as correlated changes in the mean or modal trait value(s) of the population.
342 Importantly, evolutionary and ecological tracking are interdependent, here forming a link
343 between ecology and evolution. As evolutionary tracking strengthens, ecological tracking
344 is diminished because a population that adapts quickly does not experience the same extent
345 of variation in its vital rates and parameters (here r and K) (See figure 3b,d). As ecological
346 tracking generally has a negative effect on persistence, evolutionary tracking generates a
347 benefit mitigating the population's response to ecological tracking. Given the assumptions
348 of our model (mutations per birth, mutation effect size, and population size) evolutionary
349 tracking occurs beginning at approximately $f = 0.005$. Here it can be seen that the
350 deviation between traits and the environmental optimum tends to decline at low frequencies
351 (figure 2d), leading to an increase in the population size and mean persistence times.
352 Together the evolutionary and ecological tracking lead to the U-shaped response to
353 frequency. Variation in population size is not only caused by variation of demographic
354 stochasticity between different vital rates, but also by intraspecific trait variation. Since
355 any individual can give birth in dynamic death models, they have more trait variation in
356 the autocorrelated environments, (low f) which increases the effect of maladaptation on
357 their death rate. But as the f increases the effect of maladaptation becomes the same across
358 the models.

359

360 The eco-evolutionary dynamic that is responsible for an increase in persistence times at
361 low frequencies of environmental fluctuation, also leads to a reduction in persistence time

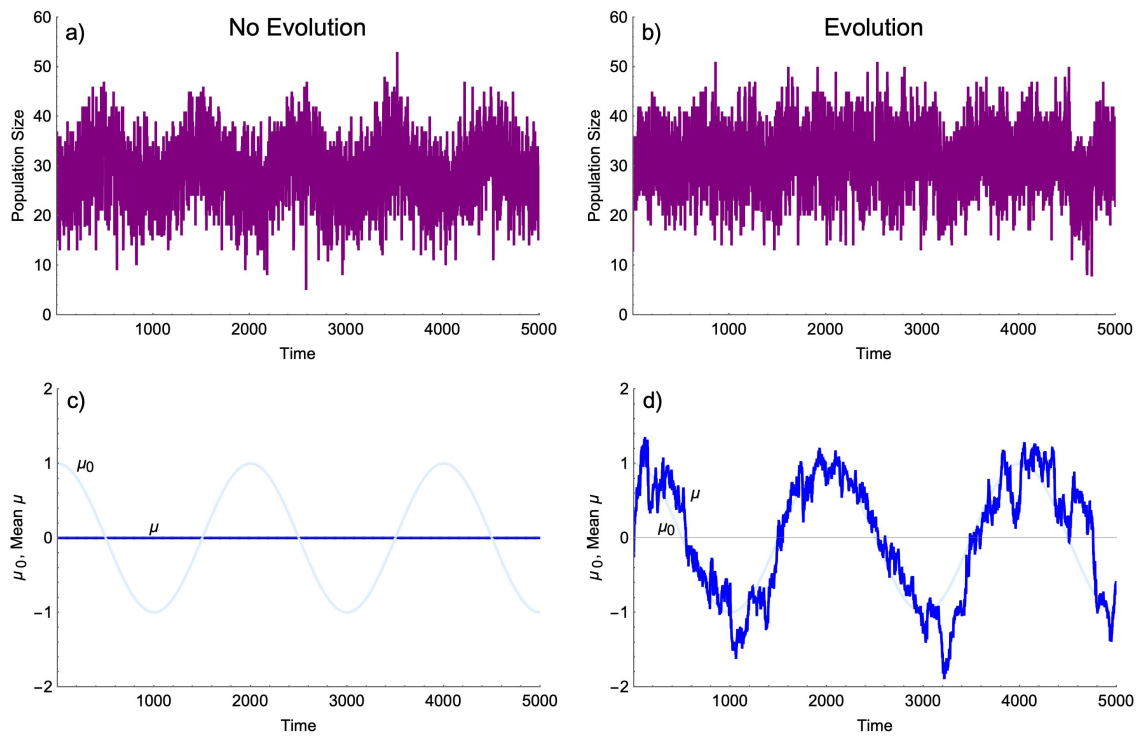
362 at intermediate and high frequencies (Figure 4). This reduction is due to mutational loading
363 (Higgins and Lynch 2001) which is here exacerbated by the fact that mutations which
364 might be immediately favorable in the population become quickly deleterious as the
365 environment oscillates. This confounding kind of evolution is most likely to occur at
366 intermediate frequencies, where complete evolutionary tracking is unlikely, but random
367 chance allows momentary “misleading” evolutionary changes to occur. We see a slight
368 inflation of the mean and range of maladaptation in our eco-evolutionary models (figure
369 2c) relative to those without evolution, reinforcing this mechanism. All of our models
370 transition from a detrimental, to a beneficial effect of the eco-evolutionary dynamic near
371 $f = 0.005$. Determining how this threshold relates to the life-history parameters of natural
372 populations will provide important information about the potential for evolution to buffer
373 populations from extinction in oscillating environments. Note that in Figure 2c, the mean
374 line is slightly decreased at low f for the death models. This is due to the higher trait
375 variation exhibited in these models as previously discussed, causing a larger deviation from
376 the optimal trait condition.



377

378 Figure 2. Population dynamics of the four model cases without and with a complete
379 evolutionary dynamic. For population size (a,b) and maladaptation (c,d), the solid lines
380 give the ensemble means of all model replicates and times and the shaded areas show the
381 25th and 75th percentiles of the distribution. For persistence time (e,f), the solid lines give
382 the means across model replicates and the shaded areas show the 25th and 75th percentiles
383 of the distribution. Maladaptation is measured as the difference between the mean
384 population trait and the environmental value. The blue line represents case 1b, the green
385 line case 1a, the orange line case 2b, and the red line case 2a, as shown in Figure 1.

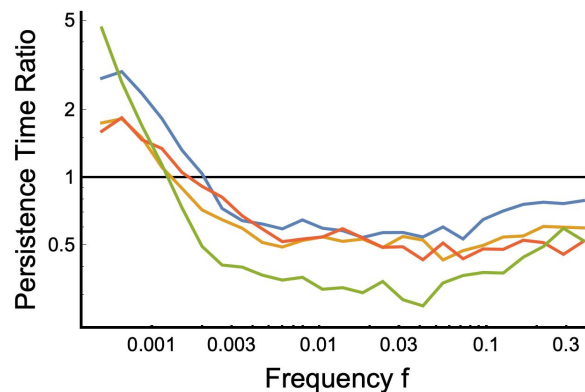
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387

388 Figure 3. Ecological tracking occurs when the population size (a) exhibits a correlated
389 pattern of variation with the environment (here μ_0) (panels a and c). In this example all
390 individuals have the same trait value, there is no evolution, and $f = 0.0005$. Panels b and
391 d show evolutionary tracking where the mean trait in the population closely follows the
392 environment, thereby dampening the ecological response to the environmental variation.

393



394

395 Figure 4. The quotient between the mean persistence time of populations that exhibited
396 evolution and the mean persistence time of populations that did not undergo evolution. For
397 values above one, evolution was beneficial for persistence, for those below one, evolution
398 had a negative impact. Evolutionary tracking increased persistence time for populations
399 when the environmental fluctuation frequency was low.

400

401 *Consequences of environmental effects on different demographic rates*

402 In natural populations we see that the demographic rates that are selected upon, and how
403 density dependence responds varies. Some populations may respond to environmental
404 change in a density independent way as in cases 1a, 2a (Dempster 1983; Brewer and Peltzer
405 2009) while some are likely to show an increase in the intensity of density dependence as
406 in cases 1b, 2b (Aanes et al. 2000; Coulson et al. 2001), with varied key demographic rates,
407 (birth or death). These results emphasize the importance of taking specific demographic
408 parameters into account into our models in the light of evolutionary rescue. Furthermore,
409 these results suggest that environmental change that primarily causes an increase in
410 mortality independent of density will be the most destructive to natural populations (Case
411 2b). We see dynamics such as this when environmental changes drive populations to
412 physiological limits, natural disasters, severe weather, and pollution. For example, a
413 change in oxygen composition in a marine ecosystem may affect a population regardless
414 of density (Brewer and Peltzer 2009), or an increase in heavy metal contamination may
415 similarly increase mortality regardless of population size (Santala and Ryser 2009).

416

417 According to our results the populations that will benefit the most from evolutionary rescue
418 will be those whose fecundity responds to an environmental change in a density dependent
419 way. This may be exemplified in cases where the availability of, or access to resources
420 diminishes or changes with environmental change. This leads to the malnutrition and lower
421 fecundity of some individuals (Jaumann and Snell-Rood 2019) but importantly in this case,
422 as the population size declines the effect of the environmental stress weakens. Note that
423 density dependence can also decrease due to environmental change in areas where the
424 change is favorable (take the case of invasive species and pests), further increasing
425 persistence potential (Ouyang et al. 2014). From these results we recommend that long-
426 term studies incorporate fine demographic data when feasible. Further analysis should be
427 done to fine tune the relevant parameters that play a role in evolutionary rescue, so that we
428 may one day be able to predict and promote evolutionary rescue in the wild.

429

430 *Consequences of our model assumptions*

431 Our modeling framework assumes asexual reproduction and a link between the
432 environment and demographic parameter that is controlled by a single trait. Most empirical
433 and theoretical work suggests that sexual recombination leads to an increased rate of
434 evolution, as it is beneficial when mutations are common and have a small effect size (Crow
435 and Kimura 1965). Recombination can also pose the opposite effect by allowing
436 maladaptive traits to persist longer in the population, leading to a greater genetic load on
437 population fitness. Incorporating recombination to assess any differences in outcome will
438 surely be relevant given the diversity of mating systems in nature. Furthermore, singular
439 step mutations are what allow the population as a whole to track the changing environment,

440 as opposed to a genotype phenotype mapping that is not one to one. This may be
441 representative of populations with a narrow genetic basis for which adaptation to the
442 environment can occur, such as what has commonly been seen in drug resistance (MacLean
443 et al. 2010). That being said, in nature some cases of environmental change will surely
444 require multiple traits to evolve for the population to persist. The utility of this model
445 though is that it is comparative, it is likely we will see the same trends in a multi-trait model
446 but this will surely be fruitful to investigate as we bring our models towards realism. This
447 will become even more relevant with the incorporation of species interactions. Competition
448 can both inhibit and promote evolutionary rescue in different cases (Osmond and de
449 Mazancourt 2013) and has shown to be a relevant component in the study of population
450 persistence.

451

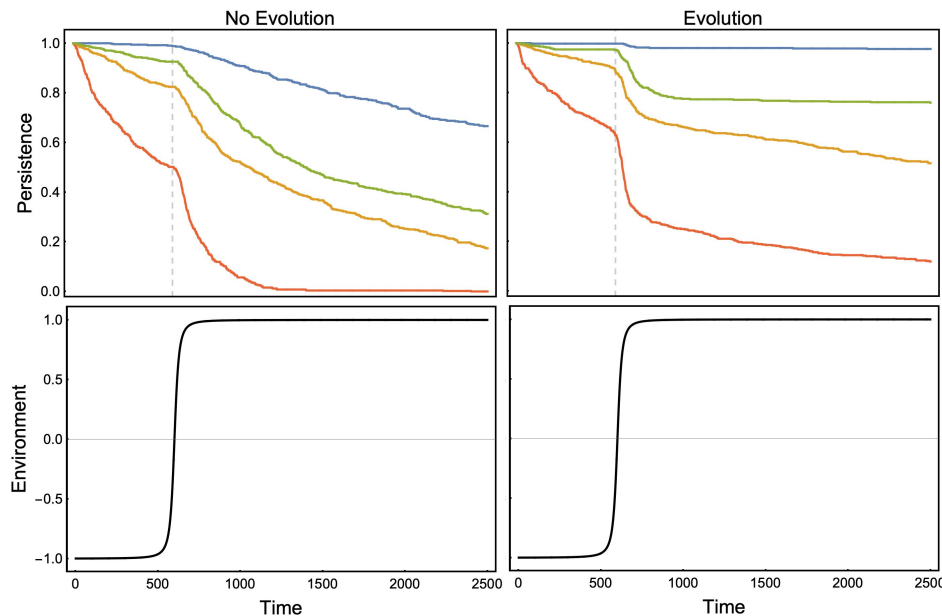
452 Lastly, the environment in this model lacks environmental stochasticity, which has been
453 shown to play a role in the potential for populations to evolve to track the changing
454 environment (Ovaskainen and Meerson 2010; Fey and Wiczyński 2017). But, because we
455 utilize a fluctuating environment instead of the single step change commonly utilized in
456 evolutionary rescue studies, we are able to characterize the ability for a population to
457 continuously adapt to a changing environment. In this way we are able to see populations
458 undergoing evolutionary rescue again and again, in order to better understand the
459 mechanisms underlying this dynamic. In environments undergoing non-cyclic changes, the
460 rate and extent of environmental change together form a critical axis on which the success
461 of evolutionary rescue (or more appropriately eco-evolutionary rescue) can be measured.
462 Generally, the potential for eco-evolutionary rescue is assessed using a singular

463 environmental change, e.g. from low to high concentrations of salt, or cold to warm
464 temperatures, (Doebeli and Dieckmann 2003; Crump et al. 2004; McCain and Grytnes
465 2010) and the typical pattern of population and trait dynamics are easily explained using
466 the concepts of ecological and evolutionary tracking applied above; when traits are able to
467 track the environmental change quickly enough, ecological changes are dampened enough
468 to prevent extinction. Thus, our model, which incorporates a cyclic environmental change,
469 is a useful predictor of how different assumptions about life history will alter the propensity
470 of eco-evolutionary rescue. We confirm that our results are not an outcome of this cyclic
471 environment, as the same persistence ranking results from a sinusoidal shift in the
472 environment (Figure 5).

473

474 The study of evolutionary rescue has increased notably in the past decade, and although
475 we have elucidated a reduced set of relevant factors, the interplay between demography
476 and evolutionary rescue is still largely unknown. We show that models with varied
477 dynamic demographic parameters with the same carrying capacities and initial conditions
478 have different probabilities of undergoing evolutionary rescue following environmental
479 change. Therefore, comparative evolutionary demography provides a lens with which we
480 can understand how different populations may be more or less likely to persist alongside
481 environmental change. As emphasized in previous studies, evolutionary rescue in these
482 models occurs when the rate of environmental change, or the fluctuation frequency is slow
483 enough for the population to evolutionarily track the changing trait optimum as shown in
484 figure 3b,d (Perron et al. 2008; Lindsey et al. 2013). Although the current model does not
485 take into account spatially heterogeneous environments or interspecific competition, it

486 provides a starting point to better understand the interplay between evolutionary
487 demography and evolution to a changing environment. We find that changing the
488 demographic parameter that selection acts on, as well as the way in which selection alters
489 density dependence, changes a populations propensity to avoid extinction via evolutionary
490 rescue.



491

492 Figure 5. The proportion of persisting populations over time. These plots portray a typical
493 evolutionary rescue scenario with a sigmoidal environment. The top panels depict the
494 proportion of surviving populations over time out of 512 replicates for case 1a (green), 1b
495 (blue), 2a (red), and 2b (yellow).

496

497 **Conclusion**

498 We show that when evolution is occurring in a system, the extinction probabilities vary
499 given different dynamic demographic parameters. This work is the first to show that
500 populations whose abundance is determined by changes in different key demographic

501 rates have different probabilities to avoid climate-induced extinction via evolution. This
502 comes into play in how well a population can evolve to have high fitness in a changing
503 environment, and the ability of a population to rebound from small population sizes. Our
504 findings show the importance of explicitly incorporating environmental change and
505 density dependence into equations describing population demographic rates. In our study
506 the environment provides the selective pressure on individuals, and unlike in previous
507 work the shape of this selective pressure is shown to differ between commonly used
508 models. This result would not have been shown had we focused on a purely ecological or
509 evolutionary model, this interplay is what allows us to make novel insights into if and
510 how population persistence will be altered by climate change. Furthermore, incorporating
511 selection and trait evolution into models on ecological time scales is an important
512 research priority. This work shows that natural populations that have different key
513 demographic rates will likely respond differently to climate change, and this information
514 should be explicitly incorporated into models that predict extinction due to climate
515 change.

516

517 In order to minimize extinction of natural populations alongside changing environmental
518 conditions such as climate change, we must be able to make decisions without complete
519 data describing future phenomena. It is therefore vital to create theory that can aid
520 scientists and wildlife managers alike in understanding how natural populations respond
521 to escalating rates of environmental challenge. This includes techniques utilizing the
522 population data we already have, to use the past as a proxy for the future, as well as
523 techniques utilizing our understanding of evolution to form ideas of how populations can

524 adapt and how we can help them to adapt to persist into the future. Our current lack of
525 understanding of the combined effect of ecological and evolutionary dynamics on the
526 outcome of climate change, poses a challenge to produce theoretical and experimental
527 work investigating these mechanisms. Already scientists are corroborating theoretical
528 hypotheses with experimental results for concepts such as rate of environmental change,
529 initial population size, and genetic variability (Bell and Gonzalez 2009, 2011; Martin et
530 al. 2013). The results provided in this study provide us with new testable hypotheses that
531 we can test utilizing experimental evolution. The comparative framework we've
532 established allows us to test the probability of population rebound post decline due to
533 environmental change between populations whose demography responds differently.

534

535 It is clear that in order to assess a population's propensity for evolutionary rescue, we must
536 pay attention to the specific life history parameters that determine population size both
537 with and without environmental change. That is, what is the key factor that determines
538 population size, what role density dependence plays and how environmental change alters
539 the vital rates and their response to density (Coulson et al. 2008). The way that the
540 environment alters population vital rates and response to density in predictive models is
541 often simplified in the literature when using data driven frameworks that predict
542 population size based on current habitat (Guisan and Zimmermann 2000; VanDerWal et
543 al. 2009; Thuiller et al. 2014), and theoretical frameworks where the environmental
544 change acts on r directly (Vasseur et al. 2011; Cropp and Norbury 2019). This can
545 conceal population response to environmental change as r is an aggregate of many

546 processes (fecundity, mortality, dispersal etc) that may respond differently to
547 environmental change.

548

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