

1 ***When do shifts in trait dynamics precede population declines?***

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17 **Abstract**

18 Predicting population responses to environmental change is an on-going challenge in
19 ecology. Studies investigating the links between fitness-related phenotypic traits and
20 demography have shown that trait dynamic responses to environmental change can
21 sometimes precede population dynamic responses, and thus, can be used as an early
22 warning signal. However, it is still unknown under which ecological and
23 evolutionary circumstances, shifts in fitness-related traits can precede population
24 responses to environmental perturbation. Here, we take a trait-based demographic
25 approach and investigate both trait and population dynamics in a density-regulated
26 population in response to a gradual change in the environment. We explore the
27 ecological and evolutionary constraints under which shifts in a fitness-related trait
28 precedes a decline in population size. We show both analytically and with
29 experimental data that under medium-to-slow rate of environmental change, shifts
30 in trait value can precede population decline. We further show the positive influence
31 of environmental predictability, average reproductive rate, plasticity, and genetic
32 variation on shifts in trait dynamics preceding potential population declines. These
33 results still hold under non-constant genetic variation and environmental
34 stochasticity. Our study highlights ecological and evolutionary circumstances under
35 which a fitness-related trait can be used as an early warning signal of an impending
36 population decline.

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39 1. Introduction

40 Exogenous pressure can force complex systems with alternative stable states
41 towards so-called tipping points, the point at which the state system can rapidly and
42 substantially change in response to a small perturbation (May 1977; Hutchings and
43 Reynolds 2004; Frank et al. 2011) . Examples of such transitions are documented
44 from rapid shifts in shrub cover in grasslands (Kéfi et al. 2007) to the collapse of
45 fisheries (Jackson et al. 2001; Frank et al. 2011), and have been shown to be
46 experimentally inducible in laboratory systems (Dai et al. 2012; Lei Dai, Korolev,
47 and Gore 2013). The non-linear nature of such transitions makes them difficult to
48 predict, but may be possible through the identification of statistical signals
49 embedded in time series data, typically termed early warning signals (EWS) (Wissel
50 1984; Dakos et al. 2008; Marten Scheffer et al. 2009). Such statistical signals arise
51 from a systems behavior prior to a critical transition (van Nes and Scheffer 2007; M.
52 Scheffer et al. 2012) – whereby it takes longer to return to it’s original equilibrium
53 state after every perturbation. This behavior of the system is known as critical
54 slowing down (CSD).

55 CSD behavior is predicted to lead to increasing variance and autocorrelation in the
56 abundance time-series in the region of a bifurcation. However, shifts in variance or
57 autocorrelation in the abundance time series might not be the only indicators of
58 whether a population is nearing a tipping point (Clements and Ozgul 2016). External
59 environmental change has been shown to also substantially affect phenotypic trait
60 distributions along with changes in demography (Traill, Schindler, and Coulson

61 2014; Pigeon et al. 2017). Phenotypic traits, for example body size, are intimately
62 linked with an individual survival and reproductive success (McNamara & Houston,
63 2007), vulnerability of a population to extinction and fluctuations in population size
64 (Olden, Hogan, and Zanden 2007; van Benthem et al. 2017). Changes in body size
65 have also been shown to influence resilience of food webs to disturbance
66 (Woodward et al. 2005). Furthermore, recent work has also suggested the inclusion
67 of body size-based measures of stability, as shifts in body size of diatoms were
68 detected before a regime shift in a lake ecosystem (Spanbauer et al. 2016). Thus,
69 tracking shifts in such fitness-related phenotypic trait values might allow us to infer
70 how stable the population is, which can inform us about an impending population
71 decline.

72 Empirical observations from experiments and natural populations have shown that
73 including information from shifts in phenotypic traits such as body size into
74 abundance-based stability indicators improves the accuracy of predictions of
75 population collapse (Clements and Ozgul 2016; Clements et al. 2017), but the
76 circumstances under which doing so is informative is still unknown. The response of
77 a population to a change in the environment can be a combination of ecological and
78 evolutionary responses governed by factors such as genetic variation or adaptive
79 plasticity (Charmantier et al. 2008; Ozgul et al. 2012). Plastic responses to a change
80 in the environment can be fast, and such responses have been shown to stabilize
81 population dynamics (Reed et al. 2010; Charmantier et al. 2008). However, if the
82 environment keeps on changing, populations might deplete its plastic capacity and
83 standing genetic variation, causing it to eventually decline. This decline in population

84 size will also be dependent on the reproductive rate i.e., whether a population is
85 growing faster or slower (Hutchings et al. 2012; Juan-Jordá et al. 2015). In addition
86 to this, due to directional change in the environment, selection on the trait will act on
87 the standing genetic variation of that trait, and higher the genetic variation faster is
88 the evolutionary response (assuming the phenotype heritable). Such theoretical
89 expectations raise important practical questions: can a shift in phenotypic trait
90 dynamics occur before an eventual decline in population size? Under what
91 circumstances is this possible? If such a shift in trait dynamics occurs, what are the
92 factors that govern the earlier occurrence of this shift?

93 To answer these questions, we used a combination of theoretical and experimental
94 approaches to understand the circumstances under which information from trait
95 values can be useful to predict a potential population decline. First, we integrated
96 quantitative genetics and population dynamics in a theoretical approach, and
97 showed both analytically and numerically whether, and under what circumstances,
98 shifts in trait dynamics can precede population declines. We then experimentally
99 test our predictions using microcosm data where replicate protist populations were
100 forced to collapse under different environmental perturbations (Clements and Ozgul
101 2016). Finally, we evaluate, through numerical simulations, how genetic variation,
102 adaptive plasticity, and reproductive rate affect when shifts in trait dynamics
103 precede decline in population size.

104 **2. Methods and modeling framework**

105 *2.1 The model*

106 In our model, we consider a closed population that has non-overlapping generations,
107 and is subjected to density-dependent population regulation. We assume in our
108 population that all individuals experience the same environment; i.e. there is no
109 spatial heterogeneity. Fitness of individuals in the population is determined by a
110 quantitative trait z that is under stabilizing selection. Under these assumptions the
111 dynamics of the population and the mean value of the trait can be written as (Chevin
112 and Lande 2010; Gomulkiewicz and Holt 1995)

$$113 \quad N_{t+1} = N_t \bar{R}_t \quad (1)$$

$$114 \quad \bar{z}_{t+1} = \bar{a}_t + \sigma_a^2 \frac{\partial \ln \bar{W}}{\partial \bar{a}} + bu_t \quad (2)$$

115 \bar{R}_t is the average fitness of the population at generation t . \bar{z}_{t+1} is the mean value of
116 the trait at generation $t+1$, \bar{a}_t is the mean breeding value of the population at
117 generation t , σ_a^2 is the additive genetic variance, $\frac{\partial \ln \bar{W}}{\partial \bar{a}}$ is the gradient of selection on
118 the mean trait \bar{z} , \bar{W} is the mean fitness due to the trait z and bu_t quantifies the
119 average plastic response of the trait (Table 1).

120 \bar{R} in equation (1) can be expanded as :

$$121 \quad \bar{R} = \int R(z)p(z)dz \quad (3)$$

122 where $R(z)$ is the absolute multiplicative fitness of an individual with trait z and $p(z)$
123 is the distribution of the quantitative trait z which is normal. $R(z)$ can further be
124 decomposed into:

$$125 \quad R(z) = R_0^{\left(1 - \frac{f(N_t)}{f(K)}\right)} W(z) \quad (4)$$

126 where, R_0 is the net reproductive rate, $\frac{f(N_t)}{f(K)}$ is the density dependence function
127 and $W(z)$ is the Gaussian stabilizing fitness function given as $W(z, \theta) = e^{-(z-\theta)^2/2w_z^2}$
128 with width w_z^2 and optimum phenotype of θ . Hence an individual's reproductive
129 fitness will thus be determined not only by how far its trait z is from the optimum
130 phenotype θ , but will also concurrently be dependent on the current density of the
131 population given by the density-dependence function.

132 Finally, the response of the primary trait z to the environment is modeled using
133 linear reaction norms (Gavrilets and Scheiner 1993). The phenotype of an individual
134 at any generation t in the population is given by

$$135 \quad z_i = a_i + bu + \epsilon \quad (5)$$

136 where a is the breeding value of the individual i , which is normally distributed with
137 mean \bar{a} and additive genetic variance of σ_a^2 . ϵ is the residual component with mean 0
138 and variance σ_ϵ^2 . The slope b in our model determines how plastic the trait is and is
139 modeled as a constant value meaning that plasticity in the trait cannot evolve.

140 Hence, variance of the phenotype z is $\sigma_z^2 = \sigma_a^2 + \sigma_\epsilon^2$ (we assume σ_ϵ^2 to be zero in our
141 model). The environment in our model determines the optimal phenotypic
142 value θ for the primary phenotype z and also cues the plastic response. θ is assumed
143 to be linearly dependent on the environment E that selects for a particular
144 phenotypic value such that at any time t , $\theta_t = BE_t$. The environmental cue
145 u quantifies how an individual on average perceives the environment. For example,
146 snow cover could be one of the environmental cues for ground squirrels to come out
147 of their hibernation that correlates with resource availability, the environmental

148 factor (Lane et al. 2012). This means that the cue u_t and the selecting environment
149 E_t are related (Charmantier et al. 2008; Reed et al. 2010). We model this relation by
150 making the environmental cue a function of the selecting environment such
151 that $u_t = f(E_t)$. In the case when u_t is a linear function of the selecting environment
152 E_t , changes in the selecting environment triggers a change in the cue response. If
153 u_t is modeled as a constant value and independent of the selecting environment E_t ,
154 then the cue response will be different to the change in the selecting environment. In
155 this case, individuals in the population will not be able to perceive changes in the
156 selecting environment.

157 Finally we can arrive at equation (2), which describes the dynamical changes in the
158 mean trait due to changes in the mean fitness \bar{W} caused by changes in the selecting
159 environment E_t . The mean fitness \bar{W} can be calculated by: $\bar{W} = \int W(z)p(z)dz =$

160
$$\sqrt{\frac{w_z^2}{\sigma_z^2 + w_z^2}} e^{-(\bar{z}_t - \theta_t)^2 / 2(w_z^2 + \sigma_z^2)}$$

161 In our model we specifically address questions linked with the decline phase of the
162 population and not evolutionary rescue. Evolutionary rescue is a long-term process,
163 which occurs when genetic evolution rescues a population from extinction in
164 response to changes in the environment. Whether this rescue happens will depend
165 on the initial decline phase of the population, as the population might collapse before
166 it can adapt to changing environmental conditions (Gonzalez et al. 2013). Hence,
167 predicting this initial decline phase is of foremost importance if one has to mitigate
168 the demographic response of the population, before evolutionary rescue takes place
169 at a later phase.

170 2.1 Analytical framework:

171 Optimal phenotypic change in our analyses is directional and given by:

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173
$$\theta_t = \begin{cases} B & , t < t_{500} \\ B E_t = B e^{-\left(\frac{t}{500}C+C\right)} & , t \geq t_{500} \end{cases} \quad (6)$$

174

175 Where $B = 2$, $E_t = e^{-\left(\frac{t}{500}C+C\right)}$, t is the time in generations and C is a parameter that

176 controls how fast the optimal phenotype changes over time. We vary C over a range

177 of values to create a gradient of environmental change from fast to slow. Without

178 loss of generality, we consider that the average trait value is at its optimum, i.e.

179 $\bar{z} = \theta_0 = B$ and the environment shifts at $t = 500$.

180 Following an environmental change scenario, shifts in trait and population dynamics

181 are calculated by $\frac{(\bar{z}_0 - \bar{z}_t)}{\bar{z}_0}$ and $\frac{(N_0 - N_t)}{N_0}$ respectively, where \bar{z}_0 is the initial average trait

182 value and \bar{z}_t is the average trait value after the optimum phenotype shifts. N_0 is the

183 abundance at carrying capacity and N_t is the abundance after the environment shifts.

184 We consider in the analytical cases below without the effect of plasticity, i.e. $b = 0$

185 (appendix A2 for plasticity affect). Hence, all the individuals in the population differ

186 only in terms of their breeding value. For analytical simplicity, we show two very

187 simplistic cases of one-generation change in trait and the population after the

188 optimum environment shifts. *Case 1*: the environmental change scenario that causes

189 $\frac{(\bar{z}_0 - \bar{z}_1)}{\bar{z}_0} > \frac{(N_0 - N_1)}{N_0}$ i.e., shift in trait value before population decline and, *Case 2*: the

190 environmental change scenario that causes $\frac{(\bar{z}_0 - \bar{z}_1)}{\bar{z}_0} < \frac{(N_0 - N_1)}{N_0}$ i.e., shift in trait value
191 after a population decline. We consider in the above cases two extreme ends of
192 environmental change: abrupt, large shift in one generation and slow, small shift in
193 one generation. In the case of abrupt and large shift in the environment, the
194 optimum phenotype is allowed to shift in *one generation* by a large magnitude to a
195 new value of $\theta_1 = 0.5$ from a value of $\theta_0 = 2$ such that, $\delta = (\theta_0 - \theta_1) = (\bar{z} - \theta_1) =$
196 1.5. Specifically, δ can be termed as the initial phenotypic lag of the mean trait to
197 optimum phenotype in 1 generation. The level of this lag is dependent on how fast
198 the optimum phenotype shifts. A shift of $\delta \geq 1.5$, or a lag of 1.5 in just *one generation*
199 causes a substantial population decline (Fig. 1). Moreover, such a jump in the
200 optimum phenotype to a new value introduces a novel optimum that is beyond the
201 distribution of the adapted trait distribution (with $\sigma_a^2 = 0.5$). In the case of slow and
202 small shift in the environment, the optimum phenotype in *one generation* is allowed
203 to shift by a very small amount, $\delta \leq 0.2$. This value corresponds to a shift in the
204 optimum that is not novel and within the realms of the adapted trait distribution.
205 We discuss the analytical results of case 1 and case 2 in the *Result* section.

206 *2.2 Numerical simulations*

207 We performed deterministic numerical simulations of the model described above.
208 We also did stochastic numerical simulations of the model (for details see appendix
209 A3). Dynamics of the trait, population and optimum environment were iteratively
210 updated using equations (1-6). We used Gompertz density function as the form of
211 density-dependence in our model simulations (Chevin and Lande 2010; Gompertz

1825). Without loss of generality, we assumed that the mean trait value is at its
optimum $\bar{z} = \theta = B$ at the start of each simulation. Environmental change was
introduced only after the population has reached its carrying capacity which was at t
 $=500$. By varying the parameter C (equation 6), we simulated a range of
environmental change scenarios: from very slow ($C=10.5$) to fast ($C=120.5$). In all of
our simulations of different rates of environmental change, the optimum
environment switched to a new value at $t = 500$. The magnitude of this switch,
however, depended on C (equation 6). For example, if $C=20.5$, the optimum took
around ~ 30 generations to switch by a magnitude of 1.5 units and if $C=120.5$, the
optimum took just ~ 5 generations to switch. Next, to quantify whether the trait or
population abundance shifted first when the environmental conditions changed, we
calculated the area under the curves (AUC) of both the trait shift $\frac{(\bar{z}_0 - \bar{z}_t)}{z_0}$ and
population shift $\frac{(N_0 - N_t)}{N_0}$ over 20 generations after the optimum environment
changed. 1-generation change was used only in the two extreme cases to elucidate
the mathematical simplicity behind the environmental change scenario under which
trait could shift before a potential population decline. AUC, on the other hand, was
used to graphically extend the analytical results of 1-generation change to 20-
generation change. AUC quantified both the magnitude and the timing of
standardized shifts. With this, we then calculated the metric, $\Delta shift = (\text{AUC of shift in}$
 $\text{mean value of the trait} - \text{AUC of population abundance shift})$. We then compared the
size of $\Delta shift$ to the rate of change in the environment (for stochastic change in the
environment see appendix A3). If $\Delta shift$ was negative, for a particular rate of change

234 in the environment, it indicated that the population shift was larger and hence the
235 population declined/shifted earlier than a shift in the mean trait value; if $\Delta shift$ was
236 positive it meant a shift in the trait value occurred before a decline/shift in
237 population size. This allowed us to quantify under what environmental change
238 scenarios (from slow to fast) we could expect shift in average trait value to occur
239 before a potential population decline. We then evaluated how the metric $\Delta shift$, for
240 the range of environmental change scenarios, was affected by factors like genetic
241 variation, strength in plasticity, reproductive rate, and environmental predictability.
242 In the appendix we show how relaxing the assumptions of constant genetic variation
243 (appendix A4) and stochastic environmental change (appendix A3) affect $\Delta shift$.

244 *2.2.1 Rate of environmental change*

245 We varied the parameter C from a value of 10.5 to 120.5 with a step size of 2 to
246 simulate a gradient of perturbations from slow to fast environmental change. We
247 then calculated from equation (6) the time in generations the optimum took to shift
248 by a magnitude of ~ 1.5 units. This ~ 1.5 unit of change in the optimum in 5
249 generations (when, $C=120.5$) or in more than ~ 30 generations (values of $C \leq 30$)
250 was enough to cause a significant population decline (Fig. 1). We then assessed how
251 $\Delta shift$ was affected by the rate of environmental change.

252 *2.2.2 Environmental predictability*

253 We simulated two specific scenarios: 1) when the cue was a linear function of the
254 optimum environment, and hence individuals of the population could perfectly

255 predict changes in the optimum environment, 2) when the cue was a constant value
256 and hence individuals had zero predictability of changes in the optimum
257 environment. We then assessed how these two scenarios of environmental
258 predictability affected $\Delta shift$.

259 *2.2.3 Genetic variation, strength of adaptive plasticity and average reproductive rate*

260 We ran a range of numerical simulations with different levels of genetic variation
261 (low to high): $\sigma_a^2 = 0.05, 0.08, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6$; low to high strength of
262 adaptive plasticity $b = 0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6$; and low to high average
263 reproductive rate $R_0 = 1.1, 1.15, 1.2, 1.25, 1.3, 1.35, 1.5$. While varying levels of
264 genetic variation from low to high, we kept adaptive plasticity strength at $b = 0.2$ and
265 R_0 at 1.2. While varying levels of b , we kept σ_a^2 at 0.5 and R_0 at 1.2. Finally, while
266 varying R_0 , we kept σ_a^2 and b at 0.5 and 0.2 respectively. For a range of
267 environmental change scenarios, we then evaluated the effect of each parameter
268 value on $\Delta shift$.

269 *2.2.4 Stochasticity in optimum phenotypic change*

270 All of the simulations and calculations of $\Delta shift$ in the above sections were
271 deterministic. However, any recorded environmental parameter in nature, always
272 fluctuates around a mean expectation over time (García Molinos and Donohue
273 2011). We thus wanted to assess whether adding stochasticity to the changes in the
274 optimum affected our deterministic simulation results. We redid the numerical
275 simulations of the above theoretical model but added stochasticity in the optimum
276 phenotypic change (for stochasticity in the growth rate, see appendix A8). For details

277 see appendix A3. We then assessed how $\Delta shift$ performed under stochasticity in
278 optimum phenotypic change and how the abovementioned factors affected $\Delta shift$.

279 *2.2.5 Changing genetic variance*

280 All of the above simulations were done assuming that genetic variation remained
281 constant. This is true when a quantitative genetic trait was assumed to be controlled
282 by infinite number of loci (Falconer and Mackay 1996). Here, we took into account
283 the decreases in genetic variation that might occur due to directional change of the
284 optimum phenotype. For an asexually reproducing population, the variance of the
285 distribution of the breeding values was given by the equation (Bürger 2000):

$$286 \quad \Delta\sigma_a^2 = -\left(\frac{\sigma_a^4}{\sigma_a^2 + w_z^2}\right) \quad (7)$$

287 We used numerical iteration to solve the change in genetic variation over time using
288 equation (7). We repeated all the simulations above and varied the levels of
289 plasticity, reproductive rate, starting genetic variation, and environmental
290 predictability, and calculated $\Delta shift$ as before (appendix A4).

291 *2.5.6. EWS*

292 We evaluated how shifts in EWS compared with shifts in mean trait in response to
293 changes in the environment. First, we showed that our model exhibits non-
294 catastrophic transcritical bifurcation (appendix A6). Next, we estimated standard
295 deviation and autocorrelation at first-lag from abundance data as two main EWS
296 indicators. Following this, shifts in EWSs and shifts in mean trait value were
297 compared by calculating a metric called $\Delta shift_{ews}$ (appendix A6.4-A7). We evaluated

298 $\Delta shift_{ews}$ for different levels of plasticity, genetic variation and reproductive rate.
299 Furthermore, we modified our model to allow for catastrophic fold bifurcation by
300 introducing an allee threshold at equation 2 (Dai et al. 2012; Hilker 2010). Similarly,
301 for this fold-bifurcation model we evaluated $\Delta shift_{ews}$ (see appendix A6-A7 for
302 details).

303 *2.3 Experimental Data*

304 In addition, we analyzed an experimental data where microcosm populations were
305 forced to collapse by varying the rate of decline in food availability (Clements &
306 Ozgul, 2016). Clements & Ozgul (2016) used replicate populations of protozoan
307 ciliate *Didinium nasutum* that fed on *Paramecium caudatum*. In the experiment, four
308 different treatments of rates of decline of prey availability were chosen: 1) fast; 2)
309 medium; 3) slow, as well as a constant prey availability as the control treatment. A
310 total of 60 replicate populations, 15 per treatment were used for the experiment. In
311 our study, we used data only from the deteriorating environment treatments (i.e.,
312 fast, medium and slow decline in prey availability). We analyzed each population's
313 abundance and mean body size time series independently. We then calculated AUC
314 and $\Delta shift$ to qualitatively verify our theoretical simulation results (see appendix A5
315 for details).

316 **3. Results**

317 *3.1 Analytical results*

318 Before a shift in the optimum environment occurred, we assume that the population
 319 is perfectly adapted to its optimum phenotype $(\theta - \bar{z}) = 0$. Considering the starting
 320 population size to be at K with no plasticity ($b = 0$), equilibrium population size at
 321 any time t from equation (1), (3) and (4) is

$$322 \quad N = \frac{w_z}{\sqrt{w_z^2 + \sigma_z^2}} K \text{ (appendix A1)}$$

323 *Case #1: Population declines before a trait shift:*

324 Let $N_0 = \frac{w_z}{\sqrt{w_z^2 + \sigma_z^2}} K$ be the population size when the population is at its equilibrium.

325 Next, when the environment changes by a large magnitude in one generation such
 326 that $\delta \geq 1.5$, the standardized population shift in one generation is (appendix A1):

$$\frac{N_0 - N_1}{N_0} = \frac{N_0 - N_0 e^{-\frac{(\delta)^2}{2w_z^2 + 2\sigma_z^2}}}{N_0} = 1 - e^{-\frac{(\delta)^2}{2w_z^2 + 2\sigma_z^2}} > 0;$$

327 and, $1 - e^{-\frac{(\delta)^2}{2w_z^2 + 2\sigma_z^2}} > \frac{(\bar{z}_0 - \bar{z}_1)}{\bar{z}_0}$

328 *Case #2: Trait shifts before population decline:*

329 When the environment shifts by a small magnitude such that: $\delta \leq 0.2$ in one
 330 generation. The standardized population shift becomes (appendix A1):

$$\frac{N_0 - N_0 e^{-\frac{(\delta)^2}{2w_z^2 + 2\sigma_z^2}}}{N_0} = \frac{N_0 - N_0}{N_0} \approx 0,$$

331 because, $e^{-\frac{(\delta)^2}{2w_z^2 + 2\sigma_z^2}} \approx 1$ as δ is very low conditional to the fact that $w_z^2 \gg \sigma_z^2$.

332 In this case, proportional shift in a trait is greater than zero and hence greater than
333 the population shift (see appendix A1).

$$334 \frac{(\bar{z}_0 - \bar{z}_1)}{\bar{z}_0} = \frac{(\theta_1 - \bar{z}_0) \left(\frac{w_z \sigma_a^2 \gamma}{\sigma_z^2 + w_z^2} \right)}{\bar{z}_0} > \frac{N_0 - N_t}{N_0} \approx 0$$

335 Our two extreme analytical cases showed that, if the optimum phenotype shifted by
336 a large magnitude in just one generation, the decline in population size preceded
337 shift in mean trait value immediately. However, this was not true in the scenario
338 when the optimum shifts by a very small magnitude over the course of a single
339 generation.

340 For the effect of adaptive plasticity see appendix A2.

341 *3.2 Simulation results*

342 *3.2.1 Environmental predictability*

343 Higher predictability of the optimum phenotypic change caused $\Delta shift$ to be positive
344 when compared with lower predictability (Fig. 2). Low predictability of the optimum
345 phenotypic change caused $\Delta shift$ to be negative even when the optimum phenotype
346 shifts by a magnitude of ~ 1.5 units in more than 15 generations (slow
347 environmental shift) (Fig. 2).

348 *3.2.2 Genetic variation*

349 Higher genetic variation σ_a^2 caused $\Delta shift$ to be positive but this happened when the
350 optimum environment shifted by a magnitude of 1.5 units in more than 15
351 generations (slow environmental shift) (Fig. 3C). If the optimum environment

352 shifted to a new value by a magnitude of 1.5 units in less than 15 generations (fast
353 shift), population size always declined before any visible shift in the trait value.

354 *3.2.3 Adaptive plasticity*

355 Values of plasticity ($b > 0.2$) caused $\Delta shift$ to be positive (i.e., trait shifted earlier than
356 population decline) even when the optimum shifted by a magnitude of 1.5 units in
357 less than 15 generations (fast shift) (Fig. 3B). However, for lower values of plasticity
358 ($b < 0.2$), earlier shift in trait value would occur before the population declined only
359 when the optimum environment shifted slowly (>15 generations) (Fig. 3B).

360 *3.2.4 Reproductive rate*

361 For R_0 of 1.2, trait shift occurred earlier than decline in population size i.e., $\Delta shift > 0$,
362 given the optimum phenotype shifted slowly (by a magnitude of 1.5 units in ~ 15
363 generations or more). If the optimum phenotype shifted faster than that, average
364 reproductive rate should have to be higher than 1.2 for $\Delta shift > 0$ and hence shift in
365 the trait value would then be informative of a population decline (Fig. 3A).

366 *3.2.5 Stochastic change in the optimum phenotype*

367 Higher σ_a^2 , higher b , higher environmental predictability, and higher R_0 substantially
368 caused $\Delta shift$ to be positive for this particular scenario (see appendix A3).

369 *3.2.6 Evolving genetic variation*

370 In comparison to simulations with constant genetic variation, $\Delta shift$ was smaller
371 (less positive) for simulations where genetic variation evolved over time. In other
372 words, $\Delta shift_{constant\ variation} > \Delta shift_{evolving\ variation}$ (see appendix A4).

373 3.2.7 EWS and shift in mean trait

374 We found that for both transcritical and fold-bifurcation models, shifts in mean trait
375 could occur significantly before shifts in the two EWS indicators (Appendix A6-A7).
376 This was particularly evident for medium to slow changes in the environment (Fig
377 A13-A16).

378 3.3 Experimental results

379 Experimental data supported our analytical and simulation results qualitatively.
380 Decline in prey availability from ~300 individuals of *P. caudatum* to zero happened
381 over a period of 10, 15 and 20 days indicating three different rates: fast, medium and
382 slow change in the environment respectively. Fast change in prey availability
383 resulted in population decline preceding shift in mean body size in 7 out of 9
384 replicates (Fig. 4A). However, during medium rate of prey decline, shift in average
385 body size preceded decline in population size in 7 out 9 replicate populations in and
386 4 out of 7 in slow decline in prey availability, qualitatively proving our analytical as
387 well as our simulation results correct (Fig. 4A).

388 4. Discussion

389 Predicting the fate of populations in response to environmental change is a key
390 challenge in ecology. Recently developed methods have suggested that tracking

391 fitness related traits might help achieve this goal (Clements and Ozgul 2016;
392 Clements et al. 2017). Our analytical and simulation results suggested that when the
393 optimum environment changes relatively slowly, shifts in average trait value may
394 occur earlier than shifts in the population abundance. However, this was affected by
395 the amount of genetic variation, strength in adaptive plasticity, environmental
396 predictability, and speed of life history.

397 In our simulations, due to higher adaptive plasticity ($b > 0.3$), shifts in the average
398 trait value occurred before a decline in population size in response to a fast change
399 in the optimum environment (i.e., shift of 1.5 magnitude by the optimum
400 environment in less than 15 generations)(Fig. 3B, Fig. A2). Such a result was
401 dependent on how predictable the environment was, as plastic response of the trait
402 was mediated by how well the cue was related to a change in the optimum
403 environment. If the cue was a function of the selecting environment, very high
404 adaptive plasticity ($b = 0.5$) would then lead to a shift in average trait value before a
405 decline in population size was observed even during a significant fast shift in the
406 optimum phenotype (Fig. 3B, $b = 0.5$).

407 While the positive influence of higher genetic variation on population persistence
408 (Willi and Hoffmann 2009) and evolutionary rescue (Hufbauer et al. 2015;
409 Gomulkiewicz, Krone, and Remien 2017) is relatively well studied, little is known
410 about its transient effect on shifts in average trait value in response to changes in
411 the optimum environment. Our result suggest that in response to a relatively slow
412 directional change in the environment, high and constant genetic variation in a

413 fitness-related trait will promote faster evolution in the average trait value and
414 consequently will cause a faster shift in the average trait value before a decline in
415 population size (Fig. 3C, Fig. A3). In addition, additive genetic variance is also
416 expected to decrease over time due to directional selection acting on the trait
417 (Barton and Keightley 2002). Here, in addition to the simulations with constant
418 genetic variation, we carried out a set of simulations where we relaxed the
419 assumption of constant genetic variation, and this slowed evolutionary change due
420 to the depletion of genetic variation caused by directional selection (Fig. A6). For this
421 reason, the magnitude of shift in average trait value was smaller and slower when
422 compared with another trait shift under the assumption of constant genetic variation
423 for the same scenarios of optimum environmental change (see appendix Fig. A6, A7).
424 Besides directional selection, a decline in population size can also lead to a decrease
425 in genetic variance (Ashander, Chevin, and Baskett 2016). Irrespective of the cause,
426 low genetic variance will impede both evolutionary rescue (Hufbauer et al. 2015;
427 Gomulkiewicz, Krone, and Remien 2017) as well as the predictability of population
428 decline with the help of trait information.

429 Deterministic and stochastic modeling of population persistence in response to a
430 changing environment had earlier revealed the positive affect of reproductive rate
431 on influencing adaptation (Yvonne and Hoffmann 2009). Earlier studies have also
432 reported that larger species tend to decline in population size more rapidly than
433 smaller species (Olden, Hogan, and Zanden 2007; Collette et al. 2011) due to
434 differences in life-history strategies and intrinsic growth rates between large and
435 small organisms (Hutchings et al. 2012). Populations of fish with slow life histories

436 (in the family Scombridae) declined faster than those which had comparatively
437 faster speed of life history (Juan-Jordá et al. 2015). Our modeling results also
438 reiterated that during a fast shift in the environment (shift of the optimum
439 environment by 1.5 units in <15 generations), slow growing populations ($R_0 < 1.2$)
440 would decline before a shift in the average trait value could be observed (Fig. 3A).
441 When we compared two populations with different reproductive rates, the
442 magnitude of $\Delta shift$ was found to be substantially larger for populations with higher
443 R_0 for a same rate of environmental shift (Fig. 3A, Fig. A9), due to the rapid declines
444 of the populations with lower R_0 .

445 Our results also suggested that environmental predictability (the correlation
446 between the cue and the optimum environment) was a key factor in determining the
447 earlier occurrence of a shift in the average trait value in response to a change in the
448 optimum environment. Such environmental predictability acted as an interactive
449 factor, determining the speed and magnitude of shifts in trait value, which was
450 driven particularly by the strength in plasticity. Earlier studies had also indicated the
451 positive interactive effects of environmental predictability and adaptive plasticity on
452 population dynamics (Reed et al. 2010; Ashander, Chevin, and Baskett 2016).

453 Introducing stochasticity in the change in the optimum phenotype or in the growth
454 rate (appendix A8) did not change our above results substantially (Fig. A4). In the
455 case of stochastic change in the optimum phenotype, environmental predictability
456 was particularly essential as the plastic response of the trait tracked the changes in
457 the optimum which led to an earlier trait shift before the population declined
458 (Fig.4B, Fig. A4).

459 EWS are shown to exist in models showing both non-catastrophic and catastrophic
460 transitions (Kéfi et al. 2013). In relation to this, our results suggest that regardless of
461 whether our model exhibited non-catastrophic transcritical or catastrophic fold
462 bifurcation, shifts in mean trait value could occur before shifts in EWS. This was
463 particularly evident for medium to slow change in the optimum environment
464 (FigA10-A16). Such a shift in mean trait value occurring before EWS, was however
465 slightly sensitive to variation in plasticity, genetic variation and net reproductive
466 rate. Nevertheless, shift in mean trait value in conjunction with shift in EWS could be
467 used as an indicator of imminent population declines (Clements and Ozgul 2016).

468 Our analytical and simulation results were qualitatively supported by experimental
469 data (Fig. 4A). In both medium and slow decline in prey availability treatments,
470 shifts in body size occurred before decline in population size. Shifts in body size in
471 response to decline in prey availability that were seen in the experimental data could
472 mostly be attributed to plasticity in body size, as the experimental population was
473 clonal. During fast decline in prey availability, the plastic response of body size over
474 time was not large enough to keep up with the pace of decline in prey availability
475 and hence could not stabilize the loss in fitness. This led to rapid decline in
476 population size before a significant body size shift. However, during medium decline
477 in prey availability, plastic shift in body size was able to track the decline in prey
478 availability in consequence of which a positive growth rate was maintained.

479 However, since the decline in prey availability continued, the plastic capacity of body
480 size in the population was depleted causing the population to eventually decline,
481 which was later than shift in body size was observed. In case of slow decline in prey

482 availability, the change was very slow that led to small plastic shifts in body size
483 before a decline in abundance was seen. These small shifts in body size were not
484 large enough in comparison to decline in abundance, which was reflected in some of
485 the replicates. Shifts in body size thus could be an obvious indicator of
486 environmental deterioration before a response in the population dynamics could be
487 observed. Whether a trait could be considered as an additional indicator of how
488 stressed a population is, would depend not only on the identity of the trait but also
489 on the kind of environmental forcing.

490 The results that we presented here were specific to the parameter space, but were
491 not restricted to any specific model system (see Chevin, Lande, and Mace 2010). In
492 our model, we made two main assumptions. Firstly, adaptive plasticity in our trait
493 remained constant and hence could not evolve. Studies have observed adaptive
494 phenotypic change without being able to attribute it to genetic change (Ghalambor et
495 al. 2007; Hendry, Farrugia, and Kinnison 2008). Our results, under the assumption of
496 constant adaptive plasticity, still held since we explicitly dealt with transient
497 dynamics after the optimum environment shifted. Secondly, we assumed linear
498 reaction norms. Nonlinear reaction norms are modeled for secondary traits that are
499 components of fitness, but such nonlinear reaction norms can evolve to linear ones
500 in the long term (Gavrilets and Scheiner 1993).

501 In conclusion, we show that shifts in average trait value could precede shifts in EWS
502 and population declines in response to a change in the optimum environment, and
503 higher levels of genetic variation, adaptive plasticity, environmental predictability,

504 and reproductive rate strengthened such an earlier shift in the average trait value.
505 Using an experimental data we also showed that shifts in average body size could
506 precede declines in population size, and hence could be indicative of a future
507 population decline. Such a shift in mean body size preceding a decline in population
508 size was possible if the change in the optimum environment was not fast relative to
509 the generation time of the organism. Thus, shifts in traits may be useful for
510 predicting population collapses in species where life histories are fast, the rate of
511 change of the environment is relatively slow, and the environmental predictability is
512 relatively high, giving hope that methods can be developed that for these signals in
513 real world populations.

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517 **6. References**

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- 672
- 673 List of tables and figures:

Parameters /variables	Description	Value

N_t	Abundance of the population at time t
$\bar{z}_t ; \bar{a}_t$	Mean trait value at time t ; mean breeding value at time t
$\sigma_z^2 ; \sigma_a^2$	Variance of the mean trait; additive genetic variance or variance of the mean breeding value	[0.05, 0.08, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6] ; [0.05, 0.08, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6]
b	Strength in phenotypic plasticity	0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6
R_0	Net reproductive rate	1.1, 1.15, 1.2, 1.25, 1.3, 1.35, 1.5
u_t	Environmental cue at time t	Case 1: -0.0001 Case 2: $-\frac{B}{2} + \frac{B}{2} e^{-\left(\frac{t}{500}C+C\right)}$ where, C=4
θ_t	Optimum trait at time t
w_z^2	Width of the Gaussian stabilizing fitness function. A measure of the strength in selection	40
z_i, a_i	Trait value for an individual i ; breeding

	value for an individual i	
ϵ	Residual component or unexplained component of a trait z	0
σ_{ϵ}^2	Variance in that residual component ϵ	0
E_t	External environmental value at time t
B	Coefficient that captures the strength in the external environmental change	2
C	Parameter that controls the rate of change in the external environment E_t	Various: 10.5 to 120.5

674

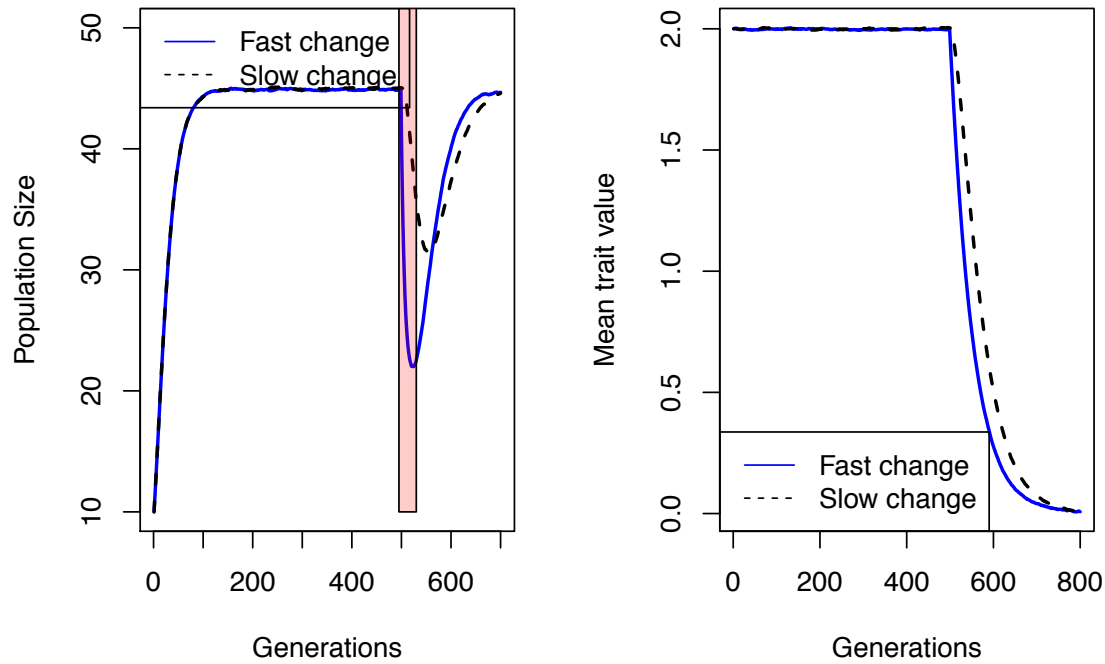
675 Table 1: List of variables and parameter values used in the model. Note that
 676 variables are not given any value, but parameters for which the model simulations
 677 are tested are given values.

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683 **Figure 1.** Population and trait dynamics under two different environmental scenarios. Left:

684 Population size declines by ~50%, when the optimum environment shifts fast ($C=120.5$;

685 blue line), whereas during slow change ($C=10.5$; dashed line) population declines but to a

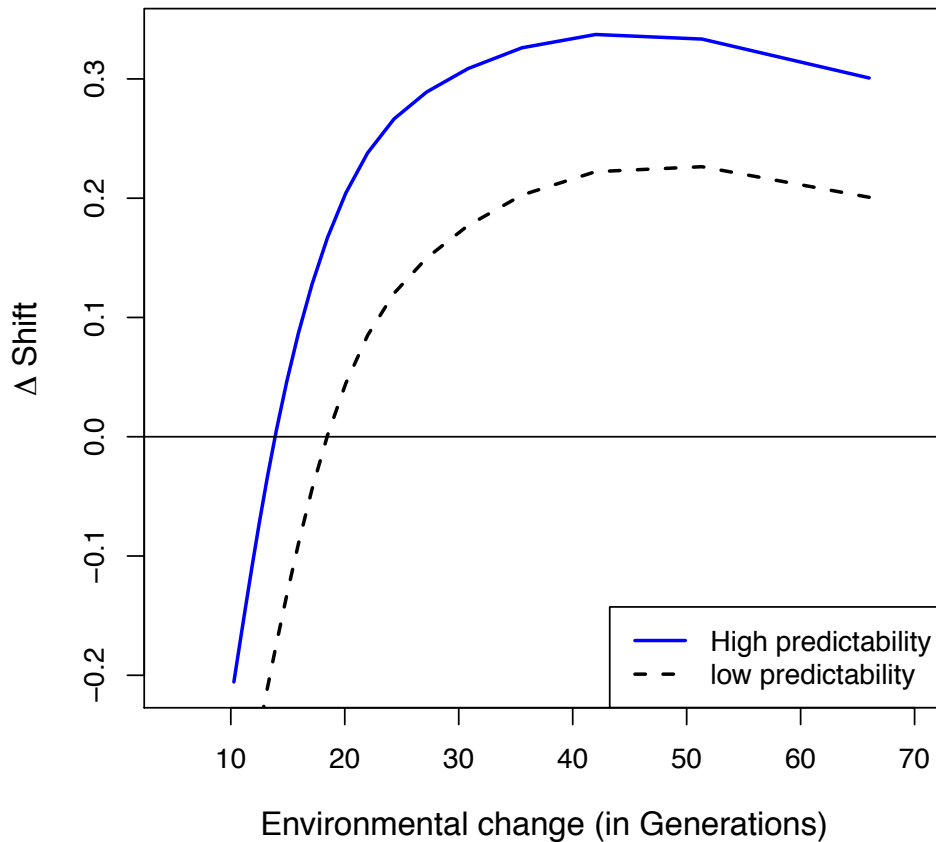
686 lesser extent. Right: Trait dynamics during fast (blue line; $C=120.5$) and slow (dashed line;

687 $C=10.5$) environmental change. Data based on deterministic simulations of the theoretical

688 model. Parameters used: $\sigma_a^2 = 0.5$; $R_0 = 1.2$; $b = 0.2$; $w_z^2 = 40$.

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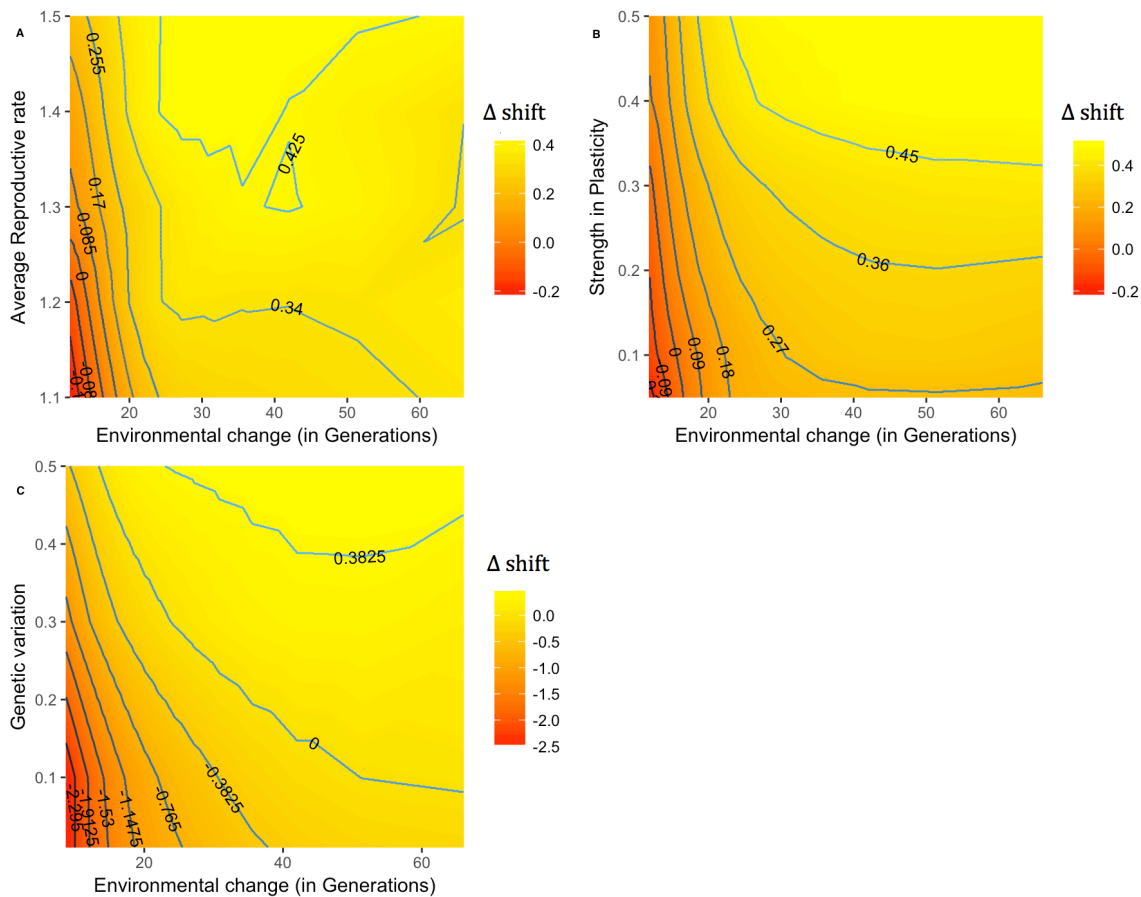
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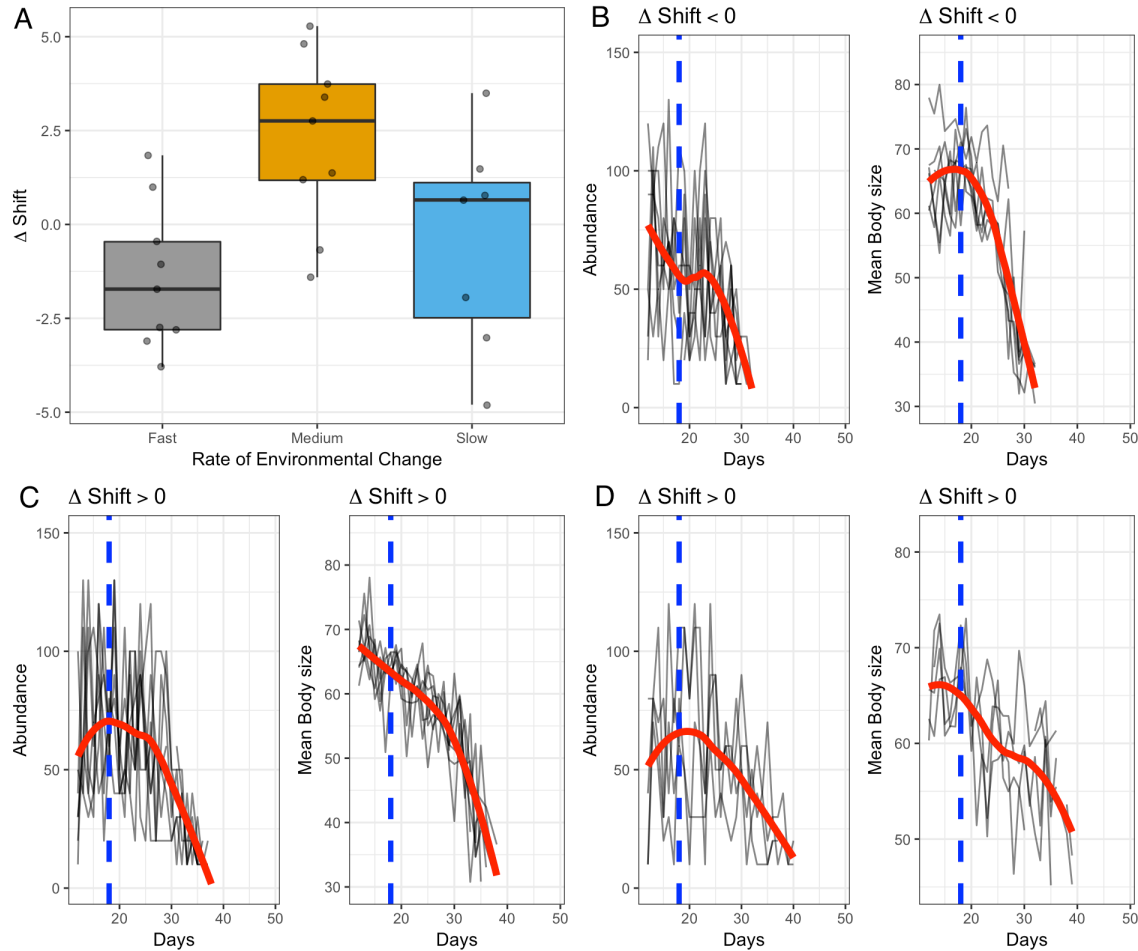
691

692 **Figure 2.** Effect of environmental predictability on the magnitude of $\Delta shift$, data from
693 numerical simulations of the theoretical model. $\Delta shift$ denotes how large and earlier the
694 shift occurs in trait dynamics before a decline in the population. If $\Delta shift$ is +ve, shift in
695 average trait value precedes decline in population size and vice versa. The X-axis denotes
696 the time in generations it takes for the optimum to change by a magnitude of 1.5 units, and
697 hence 10 in the X-axis means the optimum shifts by a magnitude of 1.5 in 10 generations
698 indicating a fast change and 60 means the optimum takes 60 generations to shift by a
699 magnitude of 1.5 units indicating a very slow change. High environmental predictability
700 (blue line) facilitates earlier occurrence of trait shift ($\Delta shift$ being +ve) compared to when

701 the environmental predictability is very low (dashed line). $\Delta shift$ is always -ve (which
702 means population declines precede mean trait shifts) when the optimum environment shifts
703 in less than or equal to 15 generations by 1.5 units. Parameters used: $\sigma_a^2 = 0.5$; $R_0 = 1.2$; $b =$
704 0.2 ; $w_z^2 = 40$.
705



706
707 **Figure 3.** Contour plot showing the effect of net reproductive rate, plasticity and genetic
708 variation on $\Delta shift$ (contour lines). Shown here are the results from numerical simulations
709 of the theoretical model. For a trait shift to be informative of a population decline, the $\Delta shift$
710 should be always greater than zero (contour line =0). The X-axis denotes the time in
711 generations it takes for the optimum to shift by a magnitude of 1.5 units.



712

713 **Figure 4.** Ability of shift in body size dynamics to precede population decline (i.e., $\Delta shift > 0$)
714 under different environmental regimes, for the experimental data from Clements & Ozgul
715 (2016). Note that $\Delta shift < 0$ if population decline precedes shift in mean body size and $\Delta shift$
716 > 0 if shift in mean body size precedes population decline. (A) $\Delta shift < 0$ for fast decline in
717 prey availability indicating that population decline preceded shift in mean body size. For
718 medium and slow decline in prey availability, $\Delta shift$ was largely positive ($\Delta shift > 0$). (B)
719 Replicate abundance and body size time-series are shown for $\Delta shift < 0$ (fast decline in prey
720 availability) and for $\Delta shift > 0$ (C and D) (Medium decline and slow decline in prey
721 availability respectively). The blue dashed line in B, C and D indicates the starting point of
722 environmental deterioration. The red line indicates *loess* smoothing across replicates.

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