HOW COMPETITION AFFECTS EVOLUTIONARY RESCUE

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Abstract

Populations facing novel environments can persist by adapting. In nature, the ability to adapt and persist will depend on interactions between coexisting individuals. Here we use an adaptive dynamic model to assess how the potential for evolutionary rescue is affected by intra- and interspecific competition. Intraspecific competition (negative density-dependence) lowers abundance, which decreases the supply rate of beneficial mutations, hindering evolutionary rescue. On the other hand, interspecific competition can aid evolutionary rescue when it speeds adaptation by increasing the strength of selection. Our results clarify this point and give an additional requirement: competition must increase selection pressure enough to overcome the negative effect of reduced abundance. We therefore expect evolutionary rescue to be most likely in communities which facilitate rapid niche displacement. Our model, which aligns to previous quantitative and population genetic models in the absence of competition, provides a first analysis of when competitors should help or hinder evolutionary rescue.

Keywords

Adaptation, adaptive dynamics, competition, environmental change, mathematical model, persistence

1 Introduction

Individuals are often adapted to their current environment [1]. When the environment changes individuals may become maladapted, fitness may drop, and population abundances may decline [2]. If the changes in the environment are severe enough, populations may go extinct. But populations can also evolve in response to the stress and thereby return to healthy abundances [3, 4]. Why some populations are capable of rescuing themselves from extinction through evolution, while others go extinct, is a central question to both basic evolutionary theory and conservation [5].

Ecological and evolutionary responses to changing environments are contingent on the community in which the change occurs [6, 7, 8, 9, 10]. A population's ability to adapt and persist in changing environments will therefore also hinge on the surrounding community [11] (see also [12], this issue). By including the ecological community in a formal theory of adaptation to changing environments, we may better predict the response of natural communities to contemporary stresses, such as invasive species [13, 14] and global climate change [15, 16].

Competition reduces population abundance [17, 18, 19, 20]. Since less abundant populations are more likely to go extinct when exposed to new environments [21, 22], competition may therefore lower the potential for evolutionary rescue. But competition can also increase selective pressure [23], speed niche expansion [24, 25, 26], and increase rates of evolution [27], possibly allowing populations to adapt to new conditions faster. These potentially contrasting effects may account for the unanticipated population dynamics and patterns of persistence in competitive communities [6] (but see [10]).

Currently, most theory on adaptation to abrupt environmental change consider only isolated populations [3, 28, 29, 30, 31, 32, 33], and many of these studies assume unbounded population growth, thus ignoring intraspecific competition as well. The studies that do consider intraspecific competition, in the form of negative density-dependence, give inconsistent conclusions, stating that density-dependence has no effect [29] or decreases [30, 34] persistence. Of the handful of studies that examine the effect of interspecific competition on adaptation to environmental change, nearly all predict slower adaptation and more extinctions (reviewed in [35]). One notable exception suggests that interspecific competition can aid persistence in a

50   continuously changing environment, by adding a selection pressure that effectively "pushes"

51   the more adapted populations in the direction of the moving environment [36].

52   Here we use the mathematical framework of adaptive dynamics to describe the evolutionary

53   and demographic dynamics of a population experiencing competition and an abrupt change in

54   the environment. Adaptive dynamics allows us to incorporate both intra- and interspecific

55   competition in an evolutionary model while maintaining analytical tractability. We assess the

56   potential for evolution to rescue populations by measuring the 'time at risk', i.e. the time a

57   population spends below a critical abundance [3]. First, we derive an expression for the 'time

58   at risk' in a population undergoing an abrupt change in isolation. We then compare our results

59   to previous studies and test the robustness of our results by relaxing a number of simplifying

60   assumptions using computer simulations. Finally, we examine how a population's ability to

61   adapt and persist to an abrupt environmental change is impacted by the presence of competing

62   species.

2   Model and Results

2.1   One-population model

65   We first examine how, in the absence of competitors, an asexual population with density- and

66   frequency-dependent population growth responds to an abrupt change in the environment.

67   We assume that each individual in the population has a trait value z, and that a phenotype's

68   growth rate is determined by both its own trait value as well as the trait value of all other

69   individuals within the population. Population dynamics are described by the logistic equation

70   (Equation 2 in [37])

$$\frac{dn_i}{dt} = n_i R\Big(1 - \frac{\int \alpha(z_i, z_j)n_j dz_j}{k(z_i, z^*)}\Big) \tag{1}$$

71   where n_i is the number of individuals with trait value z_i, R is the per capita intrinsic growth

72   rate, $\alpha(z_i, z_j)$ is the per capita competitive effect of individuals with trait z_j on individuals

73   with trait z_i, and $k(z_i, z^*)$ is the carrying capacity of individuals with trait z_i in an environment

74   where the trait value giving maximum carrying capacity is z^*. We describe carrying capacity k

75   as a Gaussian distribution (Equation 1 in [37])

$$k(z_i, z^*) = Ke^{-(z_i-z^*)^2/2\sigma_k^2} \tag{2}$$

76   where K is the maximum carrying capacity and $\sigma_k > 0$ is the 'environmental tolerance', which

77   describes how strongly carrying capacity varies with z_i. For a given deviation from z^*, smaller

78   variances σ_k^2 mean larger declines in carrying capacity k. We therefore refer to σ_k^{-2} as the

79   strength of stabilizing selection. Data on yeast responses to salt [5, 38] fit Gaussian carrying

80   capacity functions, as described by Equation 2 (ESM).

81   We do not give a specific form for intraspecific competition α, but instead give requirements

82   that are satisfied by a wide range of functions. First, we assume that individuals with the same

83   trait value compete most strongly, that is $\frac{d}{dz}\alpha(z, z) = 0$ and $\frac{d^2}{dz^2}\alpha(z, z) < 0$. This is biologically

84   reasonable and could describe, for instance, the effect of beak size on finches competing for

85   seeds, where individuals with similar sized beaks compete strongly for similar sized seeds [39].

86   And we abitrarily set $\alpha(z, z) = 1$, meaning that individuals with the same trait value take up

87   one 'unit' of carrying capacity.

88   Trait value z is assumed to be determined by a large number of loci, each with equal and

89   small effect, making the range of possible phenotypes continuous and unbounded (i.e., $z \in$

90   $\mathbb{R}$). To proceed analytically, we first assume that mutations are rare. The population remains

91   monomorphic, with all individuals having 'resident' trait value $\hat{z}$. The evolutionary trajectory

92   is determined by the per capita growth rate of rare mutants in the neighborhood of $\hat{z}$ (adaptive

93   dynamics; [40]). When mutations are sufficiently rare, evolution occurs slow enough for us to

94   consider the population at demographic equilibrium on an evolutionary timescale. This stands

95   in contrast to previous models which jointly model demography and evolution (e.g., [3, 34]).

96   The timescale separation between demography and evolution allows us to incorporate intra-

97   and interspecific competition while maintaining analytical tractability. We later use computer

98   simulations to examine how our analytical results perform when demography and evolution

99   occur on similar timescales.

100   In Appendix A we show that when $\frac{d^2}{dz^2}\alpha(z, z) < \sigma_k^{-2}$ the 'optimal trait value' z^* is both

101   convergence stable (i.e., by small steps the resident trait converges to z^*) and evolutionary

102 stable (i.e., once $\hat{z} = z^*$ no other strategies can invade; z^* is an ESS, *sensu* Maynard Smith

103 and Price [41]). We assume $\frac{d^2}{dz^2}\alpha(z,z) < \sigma_k^{-2}$ for the remainder of the paper, which means

104 frequency-dependence is weak enough [42]. Our results apply for any function α, as long as z^*

105 is both convergence and evolutionary stable.

106   Let our population begin in a constant environment with optimal trait value $z^* = z_0^*$. In

107 time, all individuals become perfectly adapted $\hat{z} = z_0^*$. The population will reach equilibrium

108 abundance $\tilde{n} = K$, and its growth rate will become zero (Figure 1). Let us call this original

109 abundance K_0.

110   INSERT FIGURE 1 HERE

111   Suppose then that the environment suddenly changes so that the new optimal trait value is

112 $z_n^* \neq z_0^*$. Our monomorphic population, with trait value $\hat{z}=z_0^*$, then immediately has equilib-

113 rial abundance $k(z_0^*, z_n^*) < K_0$ (Figure 1). The environmental change serves to decrease the

114 carrying capacity of the population. The population will initially survive the abrupt change if

115 $k(z_0^*, z_n^*) \geq 1$ or, equivalently

$$|z_0^* - z_n^*| \leq \sigma_k\sqrt{2ln(K)} \equiv \triangle z^*. \tag{3}$$

116   Note that setting $\tilde{n} \geq 1$ as the extinction threshold scales population abundance in units of

117 minimal viable population size [43, 37]. Because z_n^* is the new evolutionary and convergence

118 stable strategy, if the population survives the change it will evolve toward the new optimal trait

119 value, $\hat{z} \to z_n^*$. According to the canonical equation of adaptive dynamics [44], the monomor-

120 phic trait value $\hat{z}$ will change at rate

$$\frac{d\hat{z}}{dt} = \frac{\mu\sigma_\mu^2}{2}\tilde{n}(\hat{z}, z_n^*)g(\hat{z}, z_n^*), \tag{4}$$

121 where μ is the per capita per generation mutation rate, σ_μ^2 is the mutational variance (mutations

122 symmetrically distributed with mean of parental value), and $g(\hat{z}, z_n^*)$ is the local fitness gradient

123 (Appendix A):

$$g(\hat{z}, z_n^*) = \frac{\partial}{\partial z_m}\Big(\frac{1}{n_m}\frac{dn_m}{dt}\Big)\Big|_{z_m=\hat{z}} = \frac{-R(\hat{z} - z_n^*)}{\sigma_k^2}, \tag{5}$$

124 where n_m and z_m are a rare mutant's abundance and trait value, respectively, and $\hat{z}$ is the

125 resident trait value [40]. The local fitness gradient describes the slope of the fitness function in

126 the neighborhood of the parental trait value. Steeper slopes signify greater fitness differences

127 between individuals with similar but unequal trait values [45]. Notice that R/σ_k^2 is the strength

128 of stabilizing selection per unit time.

129 The rate of change in trait value is then:

$$\frac{d\hat{z}}{dt} = -\frac{\mu\sigma_\mu^2 R(\hat{z} - z_n^*)}{2\sigma_k^2} K e^{-(\hat{z}-z_n^*)^2/2\sigma_k^2}. \tag{6}$$

130 We cannot solve Equation 6 explicitly for $\hat{z}(t)$, but using a first-order Taylor expansion

131 we derive an approximate solution, describing evolution and demography following the abrupt

132 change (Appendix B):

$$\hat{z}(t) \approx z_n^* + (z_0^* - z_n^*)e^{\frac{-\mu\sigma_\mu^2 K_0 R}{2\sigma_k^2}t}. \tag{7}$$

133 and

$$\tilde{n}(t) = K exp\left[- \left((z_0^* - z_n^*)e^{\frac{-\mu\sigma_\mu^2 K_0 R}{2\sigma_k^2}t} \right)^2 / 2\sigma_k^2 \right]. \tag{8}$$

134 Taking the Taylor expansion about $z_0^* - z_n^* = 0$ results in the assumption that the environmental

135 change $|z_0^* - z_n^*|$ is small relative to environmental tolerance σ_k (i.e., a weak 'initial stress').

136 Our first-order approximation of the Gaussian k is therefore taken at the maximum $z = 0$,

137 which is a line with slope zero and height K_0. This means we assume mutational input μk

138 is constant at μK_0, effectively decoupling the demographic and evolutionary dynamics of the

139 recovering population. Our first-order approximation is the highest-order for which we can

140 obtain an analytical solution.

141 Now, let N_c be the abundance below which demographic or environmental stochasticity are

142 likely to cause rapid extinction [46, 3]. We use this heuristic N_c, in the place of stochastic

143 models, for simplicity. We are interested in the amount of time a population spends below this

144 threshold, i.e., how long the population is at risk of extinction.

145 The population will never be at risk of extinction if its equilibrial abundance $\tilde{n}$ remains

above the critical abundance N_c. In this model equilibrial abundance strictly increases in evo-

lutionary time in a constant environment. Abundance is therefore at a minimum immediately

following the abrupt shift in the environment. The population will avoid all chance of extinction

if $N_c < k(z_0^*, z_n^*)$ or, rearranging,

$$|z_0^* - z_n^*| < \sigma_k \sqrt{2ln\Big(\frac{K}{N_c}\Big)} \equiv \triangle z^{**}. \tag{9}$$

Here, we are most interested in the case where the population initially survives the abrupt

change but abundance drops below the critical abundance: $\triangle z^{**} < |z_0^* - z_n^*| \leq \triangle z^*$, as this is

when evolution is required to rescue populations from extinction.

From Equation 2 we can find the trait value z_{N_c} required for a carrying capacity of N_c.

Plugging z_{N_c} into Equation 7 and solving for t gives the time it will take a population to evolve

to this safe trait value z_{N_c}, which we will call the 'time at risk' t_r (Figure 2)

$$t_r = \frac{\sigma_k^2}{\mu \sigma_\mu^2 K_0 R} ln\Big[\frac{(z_0^* - z_n^*)^2}{2\sigma_k^2 ln\big(\frac{K}{N_c}\big)}\Big]. \tag{10}$$

INSERT FIGURE 2 HERE

So the time at risk t_r increases with the strength of the initial stress $|z_0^* - z_n^*|\sigma_k^{-1}$ and the ratio

of critical abundance to maximum carrying capacity N_c/K and decreases with the mutational

input μK_0, mutational variance σ_μ^2, and the strength of stabilizing selection per unit time R/σ_k^2.

Time at risk t_r is a unimodal function of environmental tolerance σ_k, with longest times at

intermediate tolerances (Figure 3). Time at risk is reduced at small and large environmental

tolerances because small tolerances cause strong selection (and hence fast evolution) and large

tolerances allow greater abundances for a given degree of maladaptation.

INSERT FIGURE 3 HERE

2.2 Comparison of one-population model to previous work

Here we compare our one-population model to previous discrete-time quantitative genetic mod-

els [3, 34]. We first show how our adaptive dynamics approach gives a qualitatively similar

description of trait dynamics over time and then compare our predictions of time at risk.

In a model without frequency- or density-dependence, Gomulkiewicz and Holt [3] describe

170 the evolutionary trajectory of the population mean trait value as a geometrical approach to the

171 optimum (Equation 5 in [3]):

$$d_t = d_0 \Big[\frac{w + (1 - h^2)P}{w + P} \Big]^t \tag{11}$$

172 where d_t is the distance of the population mean trait value from the trait value giving maximum

173 growth rate at time t, w is the variance of the growth rate function, h^2 is the trait heritability, and

174 P is the constant phenotypic variance [3]. We derive a qualitatively similar trajectory (Equation

175 7), in continuous time, from adaptive dynamics. Adaptive dynamics provides greater ecological

176 context by including intrinsic growth rate and maximum carrying capacity as parameters in the

177 evolutionary trajectory. The trajectories are identical when

$$\frac{w + (1 - h^2)P}{w + P} = Exp\Big[\frac{-\mu \sigma_\mu^2 K_0 R}{2\sigma_k^2} \Big]. \tag{12}$$

178 Gomulkiewicz and Holt [3] refer to Equation 12 as the evolutionary 'inertia' of a trait. Inertia

179 is bounded between zero and one in both models. When inertia is one there is no evolution.

180 In Gomulkiewicz and Holt [3] evolution halts when trait heritability h^2 or phenotypic variance

181 is zero. In our model, inertia is determined by mutational input μK_0, and evolution halts

182 when there are no mutations. For a given w and $h^2 \neq 0$, inertia is minimized and evolution

183 proceeds at a maximum rate in Gomulkiewicz and Holt [3] as phenotypic variance goes to

184 infinity $P \to \infty$. In our model, for a given strength of stabilizing selection per unit time R/σ_k^2,

185 inertia to approaches zero and the rate of evolution is maximized as mutational input goes to

186 infinity $\mu K_0 \to \infty$.

187   Note that to maintain analytical tractability both models assume the material which selec-

188 tion acts upon (phenotypic variance P or mutational input μK_0) is constant. Both models will

189 therefore be more accurate when the environmental change is relatively small. Large changes

190 in the environment are likely to cause strong selection and large variation in abundance, which

191 could greatly alter phenotypic variance and mutational input [30]. Since phenotypic variance

192 and mutational input are expected to decline under strong stabilizing selection and reduced

193 abundance [47], respectively, the analytical results of both models will tend to underestimate a

194 population's time at risk.

195   Our evolutionary trajectory aligns even closer with that of Chevin and Lande (Equation 10 in

196 [34]; also see Equation 18a in [48]), who incorporated both density-dependence and phenotypic

197 plasticity. The two trajectories are identical when there is constant plasticity $\varphi = 0$, additive

198 genetic variance is equivalent to the supply rate of beneficial mutations times mutational size

199 $\sigma_a^2 = \mu \sigma_\mu^2 K_0 / 2$, and the two measures of stabilizing selection strength per unit time are the

200 same $\gamma^* = R / \sigma_k^2$.

201   Although our evolutionary trajectory aligns closely with those of Gomulkiewicz and Holt

202 [3] and Chevin and Lande [34], we uncover an analytical approximation for the time at risk t_r

203 by assuming a timescale separation between demographics and evolution. Gomulkiewicz and

204 Holt [3] and Chevin and Lande [34] do not assume such a timescale separation, leading to more

205 complex population dynamics and the need to calculate t_r numerically. This makes a quantita-

206 tive comparison with our time at risk approximation impossible. However, Gomulkiewicz and

207 Holt [3] agree that the time at risk t_r should increase with initial maladaptation (i.e., magnitude

208 of environmental change) $|z_0^* - z_n^*|$ and that at high degrees of maladaptation the relationship

209 with time at risk should be close to linear (Figure 3; Figure 5A in [3]). In addition, in both

210 Gomulkiewicz and Holt [3] and Chevin and Lande [34] strengthening selection $1/\omega \to \infty$ in-

211 creases the rate of adaptation while decreasing abundance (through a decline in mean fitness).

212 Time at risk should therefore be minimized at an intermediate selection strength, as in our

213 model (Figure 3, bottom panel), although they do not explore this explicitly. Gomulkiewicz

214 and Holt [3] also argue that the time at risk t_r should decrease with the abundance before envi-

215 ronmental change, since the population declines geometrically beginning at this abundance. In

216 our model, time at risk also decreases with abundance before environmental change K_0, but for

217 a different reason. Recall that because of our first-order approximation we assume a small ini-

218 tial stress and hence a small change in abundance. This allows us to assume that mutations are

219 supplied at a constant rate μK_0, where μ is the per capita mutation rate and K_0 is the abundance

220 before environmental change. A greater abundance before environmental change K_0 therefore

221 causes faster evolution resulting in less time at risk. Finally, although

2.3 Simulations

Adaptive dynamics assumes mutations are rare enough such that, on the timescale of evolution, the population remains monomorphic (i.e., a mutation fixes or is lost before the next arises [49]) and at demographic equilibrium (i.e., demography is faster than evolution) and that mutations are small enough to allow local stability analyses to determine evolutionary stability [40, 45]. Our approximation of time at risk t_r (Equation 10) also rests on the assumption that the initial stress $|z_0^* - z_n^*|\sigma_k^{-1}$ is weak. We therefore performed computer simulations to examine how well our analytical result (time at risk t_r) holds when we relax these assumptions. To do this we varied (a) mutation rate μ and maximum carrying capacity K, (b) mutational variance σ_μ^2, and (c) the strength of the initial stress $|z_0^* - z_n^*|\sigma_k^{-1}$. Computer simulations allow multiple phenotypes to coexist and introduces stochasticity in mutation rate and size.

Simulations describe the numerical integration of Equation 1, using a 4th-order Runge Kutta algorithm with adaptive step size, and stochastic mutations. Mutations occur in a phenotype with probability $\mu n \triangle t$, where μ is the per capita per time mutation rate, n is the abundance of the phenotype, and $\triangle t$ is the realized time step. For each mutation occuring in a phenotype with trait value z, one individual is given a new trait value, randomly chosen from a normal distribution with mean z and standard deviation σ_μ. Trait values are rounded to the third decimal to prevent the accumulation of overly similar phenotypes. Phenotypes with abundance below one were declared extinct. Simulations began with the population at maximum carrying capacity K and all individuals optimally adapted with trait value $z = z_0^*$. At the timestep 500, the optimal trait value instantaneously shifted to $z_n^* \neq z_0^*$. Simulations were terminated at timestep 50000. Code available upon request; implemented in R [50].

Parameter values for μ, K, and $|z_0^* - z_n^*|\sigma_k^{-1}$ were chosen in the range of those observed for yeast exposed to increased salt concentration [5]. We estimated σ_k from Figure S1 in Bell and Gonzalez [5] (ESM).

In all simulations, the population evolved towards z_n^*, and, if successful in reaching z_n^*, remained there. Likewise, population size always approached carrying capacity, as expected (Figure 2).

The transient dynamics, however, showed varying degrees of congruence with our predic-

251 tion (Equations 7 and 8; Figure 4). In simulations the amount of standing phenotypic variance

252 increases with mutation rate μ times population size. Our timescale assumption, which im-

253 plies zero phenotypic variance, is thought to become unrealistic as $\mu K log(K)$ approaches one

254 [51]. The threshold of $\mu K log(K)$ is obtained because μK is the mutational input and $log(K)$

255 is the typical time of fixation for a successful mutant when the population is well adapted

256 [51]. Over our parameter range ($\mu = \{10^{-7}, 10^{-6}, 10^{-5}, 10^{-4}\}$, $K = \{10^4, 10^5, 10^6\}$) $\mu K log(K)$

257 seemed to be an excellent predictor of accuracy; our predictions were much more accurate when

258 $\mu K log(K) < 1$. When $\mu K log(K) > 1$ we greatly underestimated the time at risk (triangles in

259 Figure 4).

260   Mutational variance σ_μ^2 seemed to have little effect on the accuracy of our predictions, at

261 least over the range of parameter space explored here ($\sigma_\mu = \{0.01, 0.05\}$; Figure 4). However,

262 our analytical prediction did perform consistently better when the initial stress $|z_0^* - z_n^*|\sigma_k^{-1}$

263 was small, for all parameter combinations (compare black $|z_0^* - z_n^*|\sigma_k^{-1} = 1.2$ and gray $|z_0^* -$

264 $z_n^*|\sigma_k^{-1} = 2.1$ points in Figure 4).

265   INSERT FIGURE 4 HERE

2.4 Competition

267 We now introduce interspecific competition. Let the population dynamics of the focal popula-

268 tion be described by the logistic growth equation:

$$\frac{dn_i}{dt} = n_i R\Big(1 - \frac{\int \alpha(z_i, z_j)n_j dz_j + C(z_i, t)}{k(z_i, z^*)}\Big), \tag{13}$$

269 where $C(z_i, t) \geq 0$ is the effect of interspecific competition on individuals in the focal popula-

270 tion with trait value z_i at time t. We do not model the coevolution of the competitors explicitly;

271 we instead keep interspecific competition $C(z_i, t)$ as general as possible, allowing it to depend

272 on focal trait value z_i and vary in time t with any other biotic or abiotic factor (including the

273 trait values and abundance of the focal and competing populations). For evolutionary rescue

274 of the focal population, the only relevant dependency is with z_i. Our formulation allows com-

275 petition C to encompass all possible types of coevolution feedback. In fact, C could even be

276 interpreted as an abiotic selection pressure. However, for brevity, we limit our discussion to

277   C as the effect of a competitor. Previous studies have explicitly modeled the coevolution of

278   competing species in a constant environment [37, 52, 53], at the expense of analytical results.

279   All other variables in Equation 13 are defined as in the one-population case.

280   We again assume that mutations are rare, so that our focal population remains monomorphic

281   with trait value $\hat{z}$ and equilibrial abundance $\tilde{n}$. In the presence of competition, equilibrium

282   abundance of the focal population is

$$\tilde{n}(\hat{z}, z^*, t) = k(\hat{z}, z^*) - C(\hat{z}, t). \tag{14}$$

283   Comparison with the one-population case, where $\tilde{n} = k$, shows how competition reduces abun-

284   dance.

285   Now, let the competing populations coexist in a constant environment with $z^* = z_0^*$. The

286   population will not necessarily evolve towards z_0^* but to a 'competitive optimal' $z_{c,0}^*$, which

287   is the trait value which maximizes equilibrial abundance $\tilde{n}$ in the original environment (Ap-

288   pendix C). Assuming $z_{c,0}^*$ is a fitness maximum (Appendix C), the focal population will even-

289   tually evolve to the competitive optimal $\hat{z} = z_{c,0}^*$. We then let the competitive optimal change

290   abruptly, to new trait value $z_{c,n}^* \neq z_{c,0}^*$. This change could arise from a shift in competi-

291   tion C or in the optimal trait value $z^* = z_n^*$. The abundance of the focal population is now

292   $k(z_{c,0}^*, z_n^*) - C(z_{c,0}^*, t)$. The amount of competition a population feels immediately following

293   the environmental change $C(z_{c,0}^*, t)$ will depend on the type of environmental change as well

294   as the response of the competitors. Competition may be close to negligible if resources remain

295   plentiful but the abundance of competitors are greatly reduced (e.g., when a pollutant causes

296   severe mortality in the competitor). However, competition may be exceptionally strong if the

297   change in environment is a shift in available resources, so that the supply of resources is limit-

298   ing (e.g., seed size changes on an island supporting multiple species of finch [54]). Persistence

299   requires $k(z_{c,0}^*, z_n^*) - C(z_{c,0}^*, t) \geq 1$, and therefore persistence following environmental change

300   is more likely when competition $C(z_{c,0}^*, t)$ is weak.

301   In Appendix C we derive the local fitness gradient of the focal population. In the new

302   environment, with $z^* = z_n^*$, it can be written as

$$g(\hat{z}, z_n^*, t) = \frac{\partial}{\partial z_m}\Big(\frac{1}{n_m}\frac{dn_m}{dt}\Big)\big|_{z_m=\hat{z}} = R\Big[\frac{\frac{\partial}{d\hat{z}}\Big(k(\hat{z}, z_n^*) - C(\hat{z}, t)\Big)}{k(\hat{z}, z_n^*)}\Big]. \tag{15}$$

The population evolves larger population size $k - C$ until $\frac{\partial}{\partial \hat{z}}(k - C) = 0$, which occurs when the population reaches the competitive optimal in the new environment $\hat{z} = z_{c,n}^*$ (Figure 5). We assume that $z_{c,n}^*$ is a fitness maximum, such that the population remains monomorphic (Appendix C).

From Equation 15 we see that, relative to the one-population case (Equation 5), competition can alter the strength and direction of selection, depending on how competition changes with trait value (Figure 5). Competition increases the strength of selection when $|\frac{\partial}{\partial \hat{z}}(k-C)| > |\frac{\partial}{\partial \hat{z}}k|$. This is will always occur when competition selects in the same direction as carrying capacity (i.e., $\frac{\partial k}{\partial \hat{z}}$ and $\frac{\partial C}{\partial \hat{z}}$ are of different signs). Competition decreases selection when $|\frac{\partial}{\partial \hat{z}}(k - C)| < |\frac{\partial}{\partial \hat{z}}k|$, which will occur when competition weakly selects in the opposite direction to carrying capacity (i.e., $\frac{\partial k}{\partial \hat{z}}$ and $\frac{\partial C}{\partial \hat{z}}$ are of the same sign and $|\frac{\partial C}{\partial \hat{z}}|$ is small). When competition selects in the opposite direction as carrying capacity and has a stronger selective effect $|\frac{\partial C}{\partial \hat{z}}| > |\frac{\partial k}{\partial \hat{z}}|$, it will reverse the direction of selection and the population will evolve away from z_n^*. Competition has no effect on selection when it is independent of trait value $\frac{\partial C}{\partial \hat{z}} = 0$.

INCLUDE FIGURE 5 HERE

Combining Equations 14 and 15 we compute the rate of adaptation, as described by the canonical equation [44]:

$$\frac{d\hat{z}}{dt} = \frac{-\mu\sigma_\mu^2}{2}\big[k(\hat{z}, z_n^*) - C(\hat{z}, t)\big]R\Big[\frac{\frac{\partial}{d\hat{z}}\Big(k(\hat{z}, z_n^*) - C(\hat{z}, t)\Big)}{k(\hat{z}, z_n^*)}\Big]. \tag{16}$$

The rate the focal population adapts $\frac{d\hat{z}}{dt}$ depends on how competition affects abundance relative to selection. Due to the added complexity of competition we are unable to solve Equation 16 for trait value as a function of time $\hat{z}(t)$ and are therefore unable to compute a time at risk t_r, as we did in the one-population case. However, we can show when competition will help or hinder adaptation, and therefore when competition has the potential to increase or decrease the likelihood of evolutionary rescue. Rearranging Equation 16 and comparing to the one-population case (Equation 6) shows that competition will increase the rate of adaptation when

(Appendix D)

$$\left| \frac{\partial}{\partial \hat{z}} \big(k(\hat{z}, z_n^*) - C(\hat{z}, t) \big) \right| > \frac{k(\hat{z}, z_n^*)}{k(\hat{z}, z_n^*) - C(\hat{z}, t)} \left| \frac{\partial k(\hat{z}, z_n^*)}{\partial \hat{z}} \right|, \tag{17}$$

and decrease the rate of adaptation when the inequality is reversed. Competition will tend to speed adaptation when competition C is weak and gets much weaker as the focal population evolves towards $z_{c,n}^*$ (dot-dashed curve in Figure 6). Note that although competition may increase the rate of adaptation, and therefore cause a greater *rate of increase* in abundance, abundance will still be depressed by competition. Competition's effect on evolutionary rescue (the time at risk t_r) will therefore depend on both its effect on adaptation and the abundance $k - C$ relative to critical abundance N_c (bottom panel in Figure 6). As maximal abundance $K - C$ approaches the critical value N_c evolutionary rescue becomes less likely, and regardless of the rate of adaptation, when $K - C \le N_c$ evolutionary rescue is impossible.

INCLUDE FIGURE 6 HERE

3 Discussion

In nature, population abundance cannot increase indefinitely [55]. One of the main 'checks of increase' [56] is competition for resources [17, 57, 19, 58, 59]. Because populations with lower abundances are more likely to go extinct [46], any factor which limits abundance is likely to hinder persistence, especially when the environment changes [22]. However, when we consider that populations can persist in new environments by adapting [3, 5], competition has a second effect, in addition to lowering population size, which could potentially help populations persist in novel environments. Since the rate a population adapts depends on the strength of selection it experiences [60, 44], competition which increases the strength of selection may speed-up adaptation [61] possibly increasing the chances of persistence in the face of change.

Intraspecific competition often has relatively little impact on selective pressures [58, 62] (but see [63]) and therefore the effect it has on evolutionary rescue will often be determined primarily by the effect it has on abundance. Previous computer simulations have suggested that negative density-dependence will have little effect on population persistence because survival depends on the dynamics of populations which are well below carrying capacity [29]. More

353 recent analytical work has come to a different conclusion, showing that, relative to the density-

354 independent case, density-dependence can increase the rate at which abundance declines as

355 well as decrease the rate abundance recovers, therefore increasing the time a population spends

356 at risk of extinction [34]. The conflicting results are due to the different types of density-

357 dependence used in the two studies. In Boulding and Hay [29] density-dependence is linear

358 (i.e., per capita growth rate declines linearly with abundance) while in Chevin and Lande [34]

359 density-dependence is stronger than linear at low abundances (the per capita growth rate de-

360 clines logarithmically with abundance). Since it is the effect of density-dependence at low

361 abundances that is critical for population persistence, this explains why Chevin and Lande [34]

362 claim density-dependence increases the chances of extinction. A similar trend is expected in

363 biological invasions, where populations experiencing strong density-dependence at low abun-

364 dances are predicted to invade slowly [64].

365   Here we assume evolution is slow, and hence, on the timescale of evolution, populations

366 are always at carrying capacity. Carrying capacity therefore indicates how well a population

367 is adapted; populations below carrying capacity will increase in abundance without evolving,

368 and hence may not require evolutionary rescue if their carrying capacity is large enough. In our

369 model, it is the *maximum* carrying capacity that affects the potential, and need, for evolutionary

370 rescue. Since abundance asymptotically approaches maximum carrying capacity in evolution-

371 ary time (Figure 2), maximum carrying capacity will have a larger effect on the time at risk as

372 it approaches the critical abundance (Figure 3).

373   Notice that maximum carrying capacity plays both a demographic and evolutionary role;

374 for a given environmental change, larger values keep populations at larger abundances (K in

375 Equation 8) and, following the change, increase the rate of evolution (K_0 in Equation 7). Here

376 we assume greater abundances lead to faster evolution because they cause greater mutational

377 inputs. In previous models (e.g., [3, 34]), where the rate of evolution is determined by additive

378 genetic variation instead of mutational input, the relationship between population size and the

379 rate of evolution can be weaker (reviewed in [65]). Although non-additive genetic effects, such

380 as epistasis and dominance, and temporal fluctuations in abundance (leading to lower effective

381 population sizes) can weaken the relationship between population size and the rate of evolution

382 [66], they do not qualitatively alter our results, but merely lead to a slower rate of evolution

than predicted.

Given the differences between quantitative genetics and adaptive dynamics [51], our results are surprisingly consistent with previous quantitative genetic models of evolutionary rescue (e.g., [3, 34]). We derive a similar evolutionary trajectory and agree with Gomulkiewicz and Holt [3] on with how time at risk should increase with initial maladaptation and decrease with abundance before environmental change.

There is, however, one major difference between our approach and previous models of evolutionary rescue. All previous models assume the environmental change affects intrinsic growth rate, and that it is the intrinsic growth rate that must evolve fast enough to allow persistence. In our model, intrinsic growth rate R has no effect on abundance since populations are assumed to remain at demographic equilibrium, which is independent of R. In particular, the environmental change might affect R with no effect on abundance (so long as $R > 0$). Intrinsic growth rate is therefore irrelevant for evolutionary rescue in our model. Here rescue depends on the effect of the environmental change on carrying capacity k, and the evolution of k. Past models describe evolutionary rescue under r-selection while we describe evolutionary rescue under K-selection [67, 68]. Hence, our model is more applicable to situations where density-dependence remains strong following the environmental change, during subsequent adaptation. Density-dependence will remain strong when the demand for resources continues to equals the supply. Obviously, density-dependence will remain strong when an environmental change acts only to reduce the supply of resources. This describes how a population of Darwin's finches has responded to drought [54]. The drought lowered the supply of seeds the finches ate, causing a rapid decline in finch abundance. Competition for small seeds intensified following drought and the finch population remained at carrying capacity, a carrying capacity which had been reduced by decreased food supply. Density-dependence can also be maintained when an environmental change leaves the supply of resources unaffected but increases the per capita demands. For instance, if stress tolerance requires increased energetic demands, a population exposed to a stress may continue to experience strong density-dependence despite a decline in abundance and unaffected resources. This may describe the situation observed in recent experiments of evolutionary rescue in yeast populations exposed to salt, where glucose concentration was unaffected [5, 38].

Simulations indicate that our analytical approximations are sensitive to mutational input and the fixation times of new beneficial mutations. When mutations are too frequent or fixation times are too long we consistently underestimate the time at risk (Figure 4). The underestimate likely arises from the adaptive dynamic assumption that fixation occurs instantaneously and the population remains monomorphic. In simulations which permit greater polymorphism, less fit phenotypes compete with those closer to the adaptive optimum, imposing a demographic load on the population. The continued existence of less fit phenotypes slows the increase of carrying capacity, causing populations to remain at risk of extinction for longer than expected. This is similar to what, in microbial evolution, is refered to as 'clonal interference' [69]. However, many populations should conform to our low mutation input assumption. For instance, the mutations rate of *Saccharomyces cerevisiae* salt tolerance is approximately $\mu = 10^{-7}$ mutations per genome per generation [5]. Since our analytical approximations are accurate when $\mu K log(K) < 1$, our method can handle yeast populations of about one million cells or less.

Although our approximations are most sensitive to high mutational inputs and slow fixation times, our assumption that mutational input is constant throughout adaptation (similar to assuming constant phenotypic variance [48, 3]) becomes less realistic as the initial stress becomes larger (Figure 4). Assuming constant mutational input is necessary for an analytical solution, but causes us to consistently underestimate the time at risk. In reality, environmental changes will cause reductions in abundance which will decrease the supply rate of new mutations (or phenotypic variance [48]), effectively 'pulling the rug out from under evolutionary rescue' [30]. Both ours and the traditional quantitative genetic [48] analytical approximations are less accurate under strong selection [29]. Because high mutation rates, long fixation times, and large initial stresses all cause our approximation to underestimate the time at risk, our analytical results can be considered a best-case scenario for population persistence.

Competition between individuals of distinct species is likely to cause dramatic changes in selective pressures [70, 62]. If competition is strong enough to drive rapid adaptation, competitors can potentially help a population adapt and persist following an environmental change. In a continuously changing environment, computer simulations of two competing populations have shown that competition can aid the persistence of the better adapted population by increasing selective pressure, effectively "pushing" the phenotype of the better adapted population toward

the moving optimal [36]. Our results clarify this point - competition can aid population persistence when it increases the selective pressure to evolve to the new environment - and give an additional requirement: competition must increase selection pressure enough to overcome the negative effect of reduced abundance. The effect of competition on evolutionary rescue can be explained in terms of the overlap between the competitor's niche and the niche the focal population is attempting to adapt to. When the focal population is forced to adapt to a niche already occupied by a competitor (strong niche overlap), competition will hinder adaptation because competition selects in the opposite direction as the new environment (dashed curve in Figure 6). On the other hand, when the competitor has a niche which only partially overlaps the niche the focal population is attempting to adapt to, it can speed adaptation by depressing the fitness of individuals in the focal population which are farther from the new niche (dot-dashed curve in Figure 6). We can illustrate this concept by returning to the example of Darwin's finches. Drought reduced the supply of small seeds, shifting the niche available to the medium ground finch (*Geospiza fortis*) to larger seeds. In general, this caused *fortis* populations to evolve to larger size [54]. However, in the presence of the large ground finch *G. magnirostris*, who eat large seeds (strong niche overlap), larger *fortis* were outcompeted by *magnirostris*, preventing *fortis* from evolving to larger size [71, 72]. Meanwhile, in the presence of the small ground finch *G. fuliginosa*, who eat small seeds (partial niche overlap), smaller *fortis* were outcompeted by *fuliginosa*, causing *fortis* to evolve to a larger size faster than they did in the absence of competitors [61]. Populations of *fortis* approached the new adaptive peak faster when in competition with *fuliginosa* because *fuliginosa* increased selection pressure towards the peak. What remains to be seen, and what is pivotal for evolutionary rescue, is whether the increased adaptation of *fortis* in the presence of *fuliginosa* overcame the reduction in *fortis* abundance caused by competition with *fuliginosa*.

On the other hand, competition may be the very reason evolutionary rescue is required for persistence in the first place. Invasive species, for example, can greatly reduce the abundance of pre-existing competitors, putting many populations at risk of extinction (reviewed in [14]). Our results suggest that some invading populations, which are themselves the cause of extinction risk, hinder evolutionary rescue in their competitors, while other invaders may permit rapid adaptation. The model presented here may therefore help predict if an invasive species is likely

to cause niche displacement or extinction (reviewed in [13]). Since few examples of extinction are associated with competitive interactions between native and invasive species [13], invading competitors may often allow rapid adaptation.

Although we have shown that competition can help evolutionary rescue under specific circumstances, we have simultaneously shown that in other circumstances competition will surely hinder persistence. Interspecific competition is also expected to reduce rates of adaptation in the context of species' range limits [72] and gradual environmental changes in metacommunities [73]. When competition hinders adaptation, we expect evolutionary rescue to be more common in communities with reduced niche overlap, [74] or greater character displacement [75], since in these communities there should be less interspecific competition.

Coevolution can alter the demographic costs and selection pressures imposed by competition, therefore impacting population persistence [70]. In our case, altering the strength and selection pressure of competition means a shift in the height and slope of the competition curve (Figure 5), respectively, as the focal population evolves. A number of previous studies have investigated the effect of coevolution between competitors (although not in the context of evolutionary rescue; [37, 52, 53]). Here, instead of asking how a specific form of coevolution influences persistence, we ask a more general question: what types of coevolution help (or hinder) evolutionary rescue? For example, if coevolution is expected to cause strong character displacement [53], not only will the less adapted population "push" the better adapted population to even greater levels of adaptation, but the better adapted population will also "push" the less adapted population away from it, reducing the positive effect of competition on evolutionary rescue.

Although our analytical approach sometimes requires stricter assumptions than simulation studies (e.g., constant mutational input), it avoids the finite choice of parameter values demanded in simulation studies, and thereby provides more general results. For instance, our expression for time at risk (Equation 10) shows a unimodal relationship with environmental tolerance (Figure 5), indicating that extinction is most likely at intermediate tolerances. Extinction is most probable at intermediate environmental tolerances because small tolerances cause strong selection pressures and hence - if the population can survive the initial stress - fast evolution, while large tolerances allow high degrees of maladaptation without a demographic

cost. To our knowledge, this is the first time this relationship has been clearly demonstrated.

In a recent experiment of adaptation to a novel environment under competition, Collins [9] subjected pairs of competing photosynthetic microbe strains to increased carbon dioxide levels. Despite the loss of one of the competing strains part way through the experiment, the presence of a competitor at the beginning of the experiment always reduced the final abundance of the survivor. Collins [9] partitioned the effects of physiology, evolution to increased carbon dioxide levels, and competitive ability on final abundance. She found that when competition had an effect it was always opposing evolution to carbon dioxide. In other words, when competition affected adaptation it was because the superior competitor went extinct while the strain most capable of adapting to the new environment evolved slower than it would have in monoculture. A trade-off between competitive ability and the ability to adapt to abiotic change lowered the abundance of both strains, impeding evolutionary rescue of all. In our model, this amounts to a positive correlation between carrying capacity and competition during the initial stages of adaptation. When this positive correlation exists, competition will nearly always impede evolutionary rescue.

To our knowledge, this is the first analytical work to investigate the effect of interspecific competition on evolutionary rescue following an abrupt environmental change. In doing so, we have highlighted the general ecological and evolutionary settings where competition should help or hinder persistence to environmental change.

4   Acknowledgements

5   Appendix A

Here we find the singular strategy in the one-population case and evaluate its stability. Detailed methods can be found in Geritz et al. [40]. From Equation 1 the local fitness gradient is

$$\frac{\partial}{\partial z_m}\Big(\frac{1}{n_m}\frac{dn_m}{dt}\Big)\Big|_{z_m=\hat{z}} = \Big[-R\frac{\partial}{\partial z_m}\frac{\alpha(z_m,\hat{z})n_r}{k(z_m,z^*)}\Big]_{z_m=\hat{z}},\tag{A1}$$

where z_m is the trait value of a rare mutant with abundance n_m and $\hat{z}$ is the trait value of the resident with abundance n_r. Dropping the arguments of the functions and denoting $\frac{\partial}{\partial z_m}$ with prime gives

$$\frac{\partial}{\partial z_m}\Big(\frac{1}{n_m}\frac{dn_m}{dt}\Big)\Big|_{z_m=\hat{z}} = \Big[-R\Big(n_r\frac{\alpha'k-\alpha k'}{k^2}\Big)\Big]_{z_m=\hat{z}}.\tag{A2}$$

Assuming $\frac{d}{dz}\alpha(z,z)=0$ and $\alpha(z,z)=1$, evaluating at $z_m=\hat{z}$ gives

$$\frac{\partial}{\partial z_m}\Big(\frac{1}{n_m}\frac{dn_m}{dt}\Big)\Big|_{z_m=\hat{z}} = Rn_r\frac{k'}{k^2}.\tag{A3}$$

Specifying k as a Gaussian function (Equation 2) with mean z^* and variance σ_k^2,

$$\frac{\partial}{\partial z_m}\Big(\frac{1}{n_m}\frac{dn_m}{dt}\Big)\Big|_{z_m=\hat{z}} = R\frac{(\hat{z}-z^*)}{\sigma_k^2}e^{-(\hat{z}-z^*)^2/2\sigma_k^2}.\tag{A4}$$

The local fitness gradient is zero when $\hat{z}=z^*$ (i.e., z^* is the singular strategy). If z^* maximizes the local fitness gradient it is a fitness maximum and therefore evolutionary stable (ESS). If z^* minimizes the local fitness gradient it is a fitness minima and evolutionary branching may occur [40]. The singular strategy is a fitness maximum when

$$\frac{\partial^2}{\partial z_m^2}\Big(\frac{1}{n_m}\frac{dn_m}{dt}\Big)\Big|_{z_m=\hat{z}=z^*} < 0\tag{A5}$$

or, equivalently

$$\Big[-Rn_r\frac{\partial}{\partial z_m}\Big(\frac{\alpha'k-\alpha k'}{k^2}\Big)\Big]_{z_m=\hat{z}=z^*} < 0.\tag{A6}$$

Evaluating at $z_m=\hat{z}=z^*$ gives

$$-R(\alpha'' - k''/K) < 0, \tag{A7}$$

and z^* is therefore evolutionary stable when

$$\alpha'' > k''/K. \tag{A8}$$

Specifying k as Equation 2, z^* is evolutionary stable when

$$\alpha'' > -1/\sigma_k^2. \tag{A9}$$

The population will converge on the singular strategy z^* only if

$$\left[\frac{\partial^2}{\partial z_m^2}\left(\frac{1}{n_m}\frac{dn_m}{dt}\right)\right]_{z_m=\hat{z}=z^*} < \left[\frac{\partial^2}{\partial \hat{z}^2}\left(\frac{1}{n_m}\frac{dn_m}{dt}\right)\right]_{z_m=\hat{z}=z^*} \tag{A10}$$

$$-R(\alpha'' - k''/K) < 0, \tag{A11}$$

and so, if the singular point is evolutionary stable it is also convergence stable. Throughout the paper we assume Equation A11 holds to simplify our analysis of evolutionary rescue.

6   Appendix B

Here we derive approximations for the ecological and evolutionary dynamics in the one-population case (Equations 7 and 8). We first move all terms of Equation 6 with $\hat{z}$ to the left-hand side and bring dt to the right. Then taking the integral,

$$\int \frac{e^{(\hat{z}-z_n^*)^2/2\sigma_k^2}}{(\hat{z}-z_n^*)}d\hat{z} = \int \frac{-\mu\sigma_\mu^2 KR}{2\sigma_k^2}dt. \tag{B1}$$

Since there is no analytical solution for the indefinite integral on the left hand side, we use the Taylor expansion about $x=0$, $\frac{e^{x^2/a}}{x} = \sum \frac{x^{2n-1}}{n!a^n}$, with $x = \hat{z} - z_n^*$ and $a = 2\sigma_k^2$. Taking the Taylor series about $\hat{z} - z_n^* = 0$ leads us to assume a small change in abundance and hence constant mutational input μK. We therefore replace K with K_0 to indicate that mutational

input depends on the original abundance. We now have

$$\int \sum_{n=0}^{\infty} \frac{(\hat{z} - z_n^*)^{2n-1}}{n!(2\sigma_k^2)^n} d\hat{z} = \frac{-\mu\sigma_\mu^2 K_0 R}{2\sigma_k^2} t \tag{B2}$$

$$\int \left(\frac{1}{\hat{z} - z_n^*} + \frac{\hat{z} - z_n^*}{2\sigma_k^2} + \frac{(\hat{z} - z_n^*)^3}{8\sigma_k^4} + ... \right) d\hat{z} = \frac{-\mu\sigma_\mu^2 K_0 R}{2\sigma_k^2} t \tag{B3}$$

$$ln(\hat{z} - z_n^*) + \frac{(\hat{z} - z_n^*)^2}{4\sigma_k^2} + ... + C = \frac{-\mu\sigma_\mu^2 K_0 R}{2\sigma_k^2} t. \tag{B4}$$

Approximating to the first order

$$ln(\hat{z} - z_n^*) + C \approx \frac{-\mu\sigma_\mu^2 K_0 R}{2\sigma_k^2} t, \tag{B5}$$

and solving for $\hat{z}$ gives

$$\hat{z} \approx z_n^* + e^{\frac{-\mu\sigma_\mu^2 K_0 R}{2\sigma_k^2} t - C}. \tag{B6}$$

At $t = 0$ we have $\hat{z} = z_0^*$, so $C = -ln(z_0^* - z_n^*)$ and we get Equation 7:

$$\hat{z}(t) \approx z_n^* + (z_0^* - z_n^*)e^{\frac{-\mu\sigma_\mu^2 K_0 R}{2\sigma_k^2} t}. \tag{B7}$$

Subbing Equation B7 into Equation 2 gives an approximate description of population abundance across evolutionary time (Equation 8).

7 Appendix C

Here we find the singular strategies for a population experiencing interspecific competition and evaluate their stability. From Equation 13 the local fitness gradient is

$$\frac{\partial}{\partial z_m} \left(\frac{1}{n_m} \frac{dn_m}{dt} \right) \Big|_{z_m = \hat{z}} = \left[-R \frac{\partial}{\partial z_m} \left(\frac{\alpha(z_m, \hat{z})n_r + C(z_m, t)}{k(z_m, z^*)} \right) \right]_{z_m = \hat{z}}. \tag{C1}$$

where z_m and n_m are the trait value and abundance of a rare mutant, respectively, in a population with resident trait value $\hat{z}$ and abundance n_r. We drop the arguments of the functions and

567 denote $\frac{\partial}{\partial z_m}$ with prime. Expanding gives

$$\frac{\partial}{\partial z_m}\Big(\frac{1}{n_m}\frac{dn_m}{dt}\Big)\Big|_{z_m=\hat{z}} = -R\Big[n_r\frac{\alpha'k-\alpha k'}{k^2} + \frac{C'k-Ck'}{k^2}\Big]_{z_m=\hat{z}}. \tag{C2}$$

568 And from Equation 14:

$$\frac{\partial}{\partial z_m}\Big(\frac{1}{n_m}\frac{dn_m}{dt}\Big)\Big|_{z_m=\hat{z}} = -R\Big[(k-C)\frac{\alpha'k-\alpha k'}{k^2} + \frac{C'k-Ck'}{k^2}\Big]_{z_m=\hat{z}}. \tag{C3}$$

569 Evaluating at $z_m = \hat{z}$:

$$\frac{\partial}{\partial z_m}\Big(\frac{1}{n_m}\frac{dn_m}{dt}\Big)\Big|_{z_m=\hat{z}} = R\Big[\frac{\alpha'k^2-\alpha kk'-\alpha'Ck+\alpha Ck'+C'k-Ck'}{k^2}\Big]. \tag{C4}$$

570 Assuming intraspecific competition α is maximal when individuals share the same trait value,

571 $\frac{\partial}{\partial z_i}\alpha(z_i, z_i) = 0$, and $\alpha(z_i, z_i) = 1$:

$$g(\hat{z}, z^*) = \frac{\partial}{\partial z_m}\Big(\frac{1}{n_m}\frac{dn_m}{dt}\Big)\Big|_{z_m=\hat{z}} = -R\Big[\frac{k'-C'}{k}\Big]. \tag{C5}$$

572 Equation C5 determines the direction of selection. Evolution proceeds until $g(\hat{z}, z^*) = 0$,

573 in this case when $k' = C'$. The trait values giving $g(\hat{z}, z^*) = 0$ are evolutionary singular

574 strategies, which we will denote z_c^*. If z_c^* maximizes $g(\hat{z}, z^*)$, z_c^* is a fitness maximum; when

575 $\hat{z} = z_c^*$ no nearby mutant can invade and the population remains monomorphic with $\hat{z} = z_c^*$.

576 However, when z_c^* minimizes $g(\hat{z}, z^*)$, z_c^* is a fitness minima and evolutionary branching may

577 occur [40]. A singular point z_c^* is a fitness maximum when

$$\frac{\partial^2}{\partial z_m^2}\Big(\frac{1}{n_m}\frac{dn_m}{dt}\Big)\Big|_{z_m=\hat{z}=z_c^*} = -R\Big[\frac{\alpha''(k^2-Ck)+k(C''-k'')+(k')^2(k^3-Ck^2-1)}{k^2}\Big] < 0. \tag{C6}$$

578 To simplify our analysis of evolutionary rescue we assume that all singular strategies our pop-

579 ulation approaches are fitness maxima. This assumes, at $z_m = \hat{z} = z_c^*$,

$$\alpha''(k^2-Ck)+k(C''-k'')+(k')^2(k^3-Ck^2-1) > 0. \tag{C7}$$

580 We will also assume the singular strategies are convergence stable, requiring:

$$\Big[\frac{\partial^2}{\partial z_m^2}\Big(\frac{1}{n_m}\frac{dn_m}{dt}\Big)\Big]_{z_m=\hat{z}=z_c^*} < \Big[\frac{\partial^2}{\partial \hat{z}^2}\Big(\frac{1}{n_m}\frac{dn_m}{dt}\Big)\Big]_{z_m=\hat{z}=z_c^*}. \tag{C8}$$

8   Appendix D

Beginning with Equation 16, we look to find when interspecific competition speeds adaptation towards the optimal $z^* = z_n^*$. Dropping the arguments of the functions and denoting $\frac{\partial}{d\hat{z}}$ with prime, Equation 16 reads

$$\frac{d\hat{z}}{dt} = \frac{-\mu\sigma_\mu^2}{2}\big[k - C\big]R\Big[\frac{k' - C'}{k}\Big] \tag{D1}$$

$$\frac{d\hat{z}}{dt} = \frac{-\mu\sigma_\mu^2 R}{2}\Big[\frac{(k - C)(k' - C')}{k}\Big]. \tag{D2}$$

Since in the one-population case $\frac{d\hat{z}}{dt} = \frac{-\mu\sigma_\mu^2 R}{2}k'$ (Equation 6), competition will speed evolution when

$$\Big|\frac{(k - C)(k' - C')}{k}\Big| > |k'|. \tag{D3}$$

Since k and $k - C$ must be positive for the population to persist,

$$|k' - C'| > \frac{k}{k - C}|k'|, \tag{D4}$$

yielding Equation 17.

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9 Figure captions

Figure 1: Our initially adapted population is monomorphic for the optimal phenotype in the original environment $\hat{z}=z_0^*$ (gray). When the environment changes, the carrying capacity function shifts (black). The new carrying capacity of our population $K_n = k(z_0^*, z_n^*)$ is the height of the intersection of the original trait value z_0^* and the new carrying capacity function. The population evolves towards the new optimal phenotype z_n^*. The population is at risk of extinction while its abundance is less than N_c, or equivalently, while $\hat{z}<z_{N_c}$.

Figure 2: Adaptation following an abrupt change in the environment. (*Top*) Population trait value $\hat{z}$ evolves towards the new optimal z_n^* (Equation 7). The time it takes to evolve a trait value z_{N_c}, which gives a critical abundance N_c, is the expected 'time at risk' t_r (Equation 10). (*Bottom*) Population abundance $\tilde{n}$ increases as the population adapts to the new environment (Equation 8). Solid lines are analytical predictions (Equations 7 and 8). Greyscale is trait value weighted by abundance in a computer simulation, with dark common and white rare. The thick dashed line is total abundance at each time step in simulation. The observed time at risk is denoted $t_{r_{obs}}$.

Figure 3: (*Top*) Time at risk t_r (Equation 10) increases monotonically with the magnitude of environmental change $|z_0^*$-$z_n^*|$. Magnitudes of change smaller than $\triangle z^{**}$ are not large enough to put the population at risk of extinction (Equation 9) and magnitudes of change larger than $\triangle z^*$ cause immediate extinction (Equation 3). (*Middle*) Time at risk t_r increases as the critical abundance N_c approaches maximum abundance K. As the critical abundance approaches the maximum abundance, $N_c/K \rightarrow 1$, the ratio has a stronger effect on the time at risk. (*Bottom*) Time at risk t_r is a unimodal function of 'environmental tolerance' σ_k, where extinction is most likely at intermediate values. We must have $\sigma_k>\sigma_k^*$ for the population to survive the initial change in the environment and $\sigma_k<\sigma_k^{**}$ for the population abundance to drop below N_c (σ_k^* and σ_k^{**} are derived by rearranging Equations 3 and 9, respectively).

Figure 4: Accuracy of analytical prediction, in the one-population case. Each point represents the mean $\pm$ SE for ten replicated simulation runs. Solid line is 1:1 line; points falling on line represent perfect predictions of time at risk t_r. Squares: $\mu K log(K) \leq$0.1; Circles: $\mu K log(K) \leq$1; Triangles: $\mu K log(K) >$1; Black: $|z_0^*-z_n^*|\sigma_k^{-1}$=1.2; Grey: $|z_0^*-z_n^*|\sigma_k^{-1}$=2.1.

778 Parameters: $\mu=\{10^{-7}, 10^{-6}, 10^{-5}, 10^{-4}\}$, $K=\{10^4, 10^5, 10^6\}$, $\sigma_\mu=\{0.01, 0.05\}$, $R=1$, $\sigma_k=1$,

779 $\sigma_\alpha=1.5$, and N_c is 1000 greater than the minimum abundance of each run.

780 Figure 5: Selection pressures from carrying capacity and competition. The population evolves

781 to increase population size according to Equation 15. Population size is carrying capacity minus

782 competition $k - C$ (solid curve minus dashed curve). Populations can persist in communities

783 only when they have positive population size (region of persistence; solid line higher than the

784 dashed line). The selection pressure in the new environment is proportional to the selection for

785 carrying capacity (slope of solid curve) minus the selection for competition (slope of dashed

786 curve). The population will therefore evolve towards the trait value for which the slopes of the

787 two curves are equal $\hat{z} \to z^*_{c,n}$. The effective selection pressure will depend on the shape of the

788 two curves and the position of the population in trait space. (*A*) Competition increases selection

789 pressure. Competition decreases as carrying capacity increases, meaning both carrying capac-

790 ity and competition select in the same direction. (*B*) Competition reduces selection pressure.

791 Competition increases as carrying capacity increases, meaning carrying capacity and compe-

792 tition exert opposing selection pressures. Note that if the competition curve was steeper than

793 carrying capacity competition could reverse the direction of evolution. (*C*) Competition affects

794 all phenotypes equally, and therefore has no effect on selection pressure. (*D*) Competition in-

795 creases or decreases selection pressure. When $\hat{z} < z^*_{c,n}$ competition and carrying capacity exert

796 opposing selection pressures. When $\hat{z} > z^*_n$ competition and carrying capacity select in the

797 same direction, towards $z^*_{c,n}$, until $\hat{z} = z^*_n$. Competition and carrying capacity will then exert

798 opposing selection pressures as the population approaches $z^*_{c,n}$.

799 Figure 6: Competition can help or hinder evolutionary rescue. (*Top*) Carrying capacity k (solid

800 curve) as a function of trait value $\hat{z}$ and two competition C scenarios: complete niche overlap

801 (dashed curve) or partial niche overlap (dot-dashed curve). (*Middle*) With complete niche over-

802 lap (dashed curve) competition increases as the population adapts, and the population therefore

803 adapts slower than it would without competition (solid curve). With partial niche overlap (dot-

804 dashed curve) competition decreases as the population adapts, and the population therefore

805 adapts faster. (*Bottom*) The time a population spends at risk of extinction (the time abundance

806 $\tilde{n}$ is below critical abundance N_c) depends on competition's effect on abundance and evolution

807   as well as on the value of the critical abundance. For instance, when the critical abundance

808   is low $N_{c,low}$ both competition scenarios increase the time at risk relative to when there is no

809   competition (solid curve) because they depress the focal population's abundance. However,

810   when the critical abundance is high $N_{c,high}$ partial niche overlap (dot-dashed curve) decreases

811   the time at risk relative to the no competition case (solid curve) because it sufficiently increases
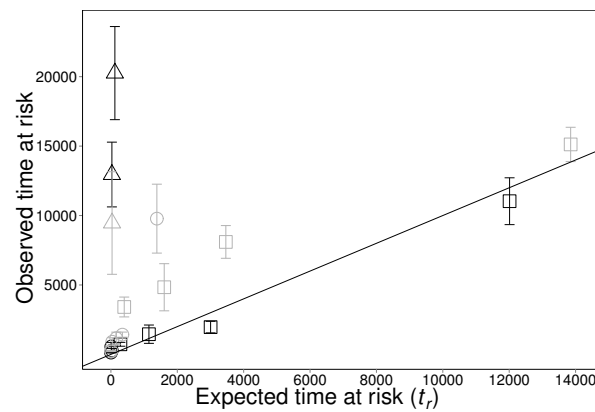
812   the rate of adaptation.

813 # 10   Figures
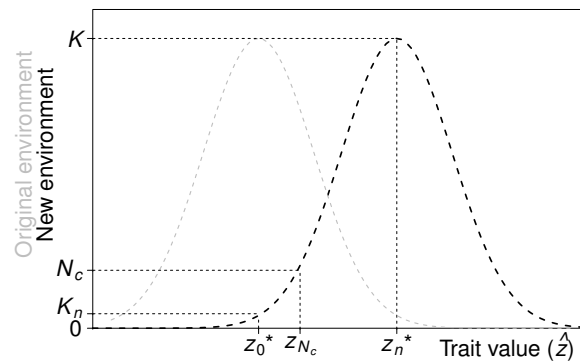
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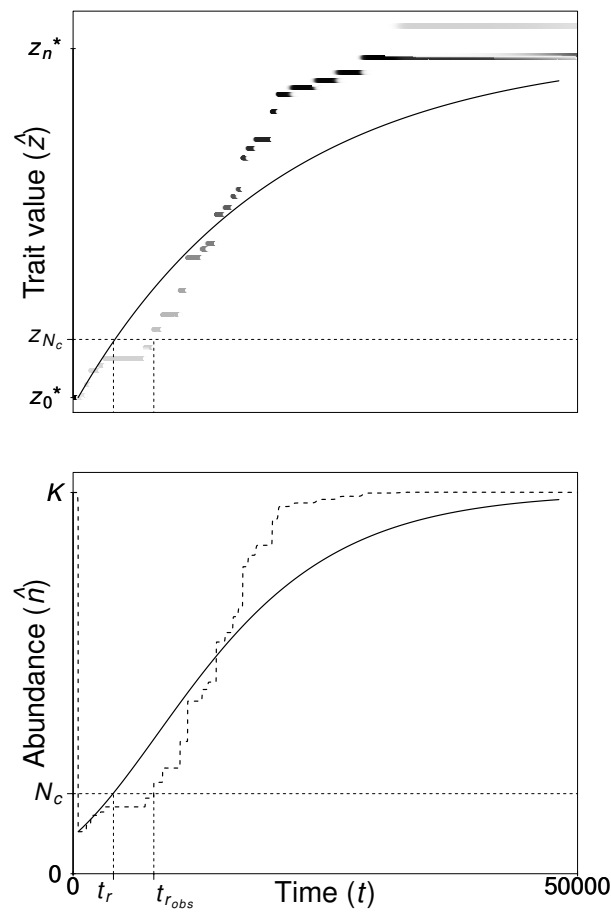
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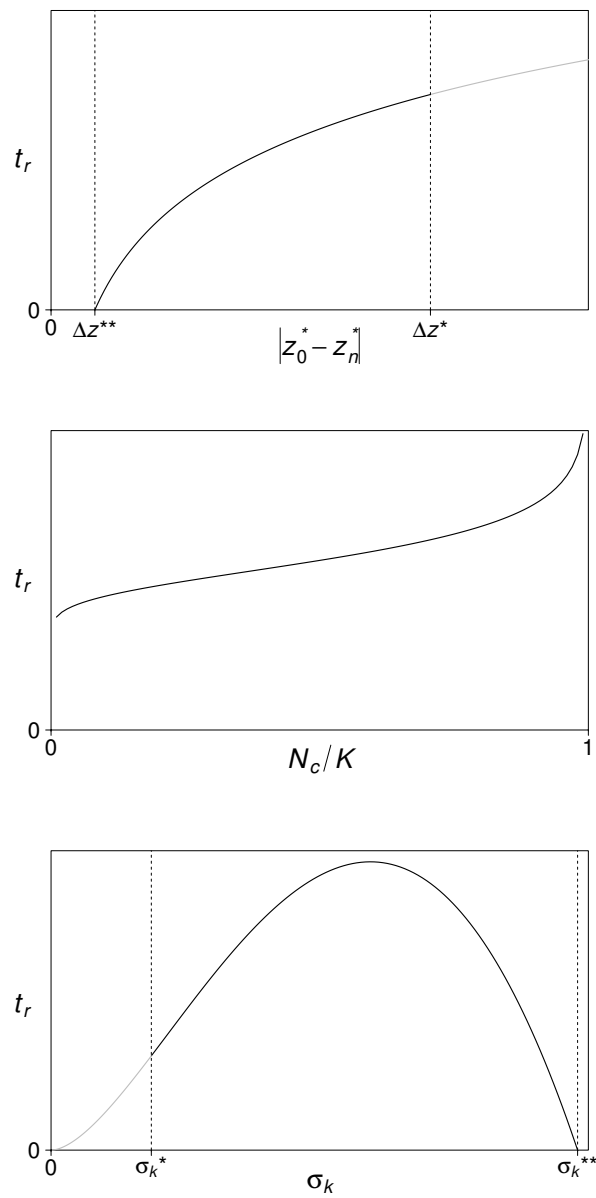
Figure 3:

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