

1 HOW COMPETITION AFFECTS EVOLUTIONARY RESCUE

2 Matthew Miles Osmond* & Claire de Mazancourt

3 Redpath Museum, McGill University, 859 Sherbrooke St. W, Montreal, QC, Canada H3A 0C4

4 *Correspondence: tel:+1 514 398 5965; fax:+1 514 398 5069; matthew.osmond@mail.mcgill.ca

5 **Abstract**

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

18 **Keywords**

19 **Adaptation, adaptive dynamics, competition, environmental change, mathematical model,**
20 **persistence**

21 **1 Introduction**

22 Individuals are often adapted to their current environment [1]. When the environment changes
23 individuals may become maladapted, fitness may drop, and population abundances may decline
24 [2]. If the changes in the environment are severe enough, populations may go extinct. But
25 populations can also evolve in response to the stress and thereby return to healthy abundances
26 [3, 4]. Why some populations are capable of rescuing themselves from extinction through
27 evolution, while others go extinct, is a central question to both basic evolutionary theory and
28 conservation [5].

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

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

42 Currently, most theory on adaptation to abrupt environmental change consider only isolated
43 populations [3, 28, 29, 30, 31, 32, 33], and many of these studies assume unbounded popu-
44 lation growth, thus ignoring intraspecific competition as well. The studies that do consider
45 intraspecific competition, in the form of negative density-dependence, give inconsistent con-
46 clusions, stating that density-dependence has no effect [29] or decreases [30, 34] persistence.
47 Of the handful of studies that examine the effect of interspecific competition on adaptation to
48 environmental change, nearly all predict slower adaptation and more extinctions (reviewed in
49 [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.

63 **2 Model and Results**

64 **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])

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

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])

$$k(z_i, z^*) = K e^{-(z_i - z^*)^2 / 2\sigma_k^2} \quad (2)$$

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 arbitrarily 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

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

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, $\hat{z} \rightarrow z_n^*$. According to the canonical equation of adaptive dynamics [44], the monomor-
 120 phic trait value \hat{z} will change at rate

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

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):

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

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:

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

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):

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

133 and

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

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 equilibrated abundance \tilde{n} remains

146 above the critical abundance N_c . In this model equilibrium abundance strictly increases in evo-
 147 lutionary time in a constant environment. Abundance is therefore at a minimum immediately
 148 following the abrupt shift in the environment. The population will avoid all chance of extinction
 149 if $N_c < k(z_0^*, z_n^*)$ or, rearranging,

$$|z_0^* - z_n^*| < \sigma_k \sqrt{2 \ln \left(\frac{K}{N_c} \right)} \equiv \Delta z^{**}. \quad (9)$$

150 Here, we are most interested in the case where the population initially survives the abrupt
 151 change but abundance drops below the critical abundance: $\Delta z^{**} < |z_0^* - z_n^*| \leq \Delta z^*$, as this is
 152 when evolution is required to rescue populations from extinction.

153 From Equation 2 we can find the trait value z_{N_c} required for a carrying capacity of N_c .
 154 Plugging z_{N_c} into Equation 7 and solving for t gives the time it will take a population to evolve
 155 to this safe trait value z_{N_c} , which we will call the ‘time at risk’ t_r (Figure 2)

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

156 INSERT FIGURE 2 HERE

157 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
 158 of critical abundance to maximum carrying capacity N_c/K and decreases with the mutational
 159 input μK_0 , mutational variance σ_μ^2 , and the strength of stabilizing selection per unit time R/σ_k^2 .
 160 Time at risk t_r is a unimodal function of environmental tolerance σ_k , with longest times at
 161 intermediate tolerances (Figure 3). Time at risk is reduced at small and large environmental
 162 tolerances because small tolerances cause strong selection (and hence fast evolution) and large
 163 tolerances allow greater abundances for a given degree of maladaptation.

164 INSERT FIGURE 3 HERE

165 2.2 Comparison of one-population model to previous work

166 Here we compare our one-population model to previous discrete-time quantitative genetic mod-
 167 els [3, 34]. We first show how our adaptive dynamics approach gives a qualitatively similar
 168 description of trait dynamics over time and then compare our predictions of time at risk.

169 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]):

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

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

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

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 $P \rightarrow \infty$. 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 $\mu K_0 \rightarrow \infty$.

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 $1/\omega \rightarrow \infty$ 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 $\mu n \Delta t$, where μ is the per capita per time mutation rate, n is the abundance of the phenotype, and Δt is the realized time step. For each mutation occurring 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

266 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:

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

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 equilibrium abundance \tilde{n} . In the presence of competition, equilibrium
 282 abundance of the focal population is

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

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 equilibrium 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

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

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

307 From Equation 15 we see that, relative to the one-population case (Equation 5), competition
 308 can alter the strength and direction of selection, depending on how competition changes with
 309 trait value (Figure 5). Competition increases the strength of selection when $|\frac{\partial}{\partial \hat{z}}(k - C)| > |\frac{\partial}{\partial \hat{z}}k|$.
 310 This is will always occur when competition selects in the same direction as carrying capacity
 311 (i.e., $\frac{\partial k}{\partial \hat{z}}$ and $\frac{\partial C}{\partial \hat{z}}$ are of different signs). Competition decreases selection when $|\frac{\partial}{\partial \hat{z}}(k - C)| <$
 312 $|\frac{\partial}{\partial \hat{z}}k|$, which will occur when competition weakly selects in the opposite direction to carrying
 313 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
 314 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
 315 reverse the direction of selection and the population will evolve away from z_n^* . Competition
 316 has no effect on selection when it is independent of trait value $\frac{\partial C}{\partial \hat{z}} = 0$.

317 INCLUDE FIGURE 5 HERE

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

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

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

327 (Appendix D)

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

328 and decrease the rate of adaptation when the inequality is reversed. Competition will tend
 329 to speed adaptation when competition C is weak and gets much weaker as the focal popula-
 330 tion evolves towards $z_{c,n}^*$ (dot-dashed curve in Figure 6). Note that although competition may
 331 increase the rate of adaptation, and therefore cause a greater *rate of increase* in abundance,
 332 abundance will still be depressed by competition. Competition's effect on evolutionary rescue
 333 (the time at risk t_r) will therefore depend on both its effect on adaptation and the abundance
 334 $k - C$ relative to critical abundance N_c (bottom panel in Figure 6). As maximal abundance
 335 $K - C$ approaches the critical value N_c evolutionary rescue becomes less likely, and regardless
 336 of the rate of adaptation, when $K - C \leq N_c$ evolutionary rescue is impossible.

337 INCLUDE FIGURE 6 HERE

338 3 Discussion

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

348 Intraspecific competition often has relatively little impact on selective pressures [58, 62]
 349 (but see [63]) and therefore the effect it has on evolutionary rescue will often be determined
 350 primarily by the effect it has on abundance. Previous computer simulations have suggested that
 351 negative density-dependence will have little effect on population persistence because survival
 352 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

383 than predicted.

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

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

413 Simulations indicate that our analytical approximations are sensitive to mutational input
414 and the fixation times of new beneficial mutations. When mutations are too frequent or fixation
415 times are too long we consistently underestimate the time at risk (Figure 4). The underestimate
416 likely arises from the adaptive dynamic assumption that fixation occurs instantaneously and the
417 population remains monomorphic. In simulations which permit greater polymorphism, less fit
418 phenotypes compete with those closer to the adaptive optimum, imposing a demographic load
419 on the population. The continued existence of less fit phenotypes slows the increase of carrying
420 capacity, causing populations to remain at risk of extinction for longer than expected. This is
421 similar to what, in microbial evolution, is referred to as ‘clonal interference’ [69]. However,
422 many populations should conform to our low mutation input assumption. For instance, the
423 mutations rate of *Saccharomyces cerevisiae* salt tolerance is approximately $\mu = 10^{-7}$ muta-
424 tions per genome per generation [5]. Since our analytical approximations are accurate when
425 $\mu K \log(K) < 1$, our method can handle yeast populations of about one million cells or less.

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

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

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

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

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

476 Although we have shown that competition can help evolutionary rescue under specific cir-
477 cumstances, we have simultaneously shown that in other circumstances competition will surely
478 hinder persistence. Interspecific competition is also expected to reduce rates of adaptation in
479 the context of species' range limits [72] and gradual environmental changes in metacommun-
480 ities [73]. When competition hinders adaptation, we expect evolutionary rescue to be more
481 common in communities with reduced niche overlap, [74] or greater character displacement
482 [75], since in these communities there should be less interspecific competition.

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

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

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

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

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

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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

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

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

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

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

$$\frac{\partial}{\partial z_m} \left(\frac{1}{n_m} \frac{dn_m}{dt} \right) \Big|_{z_m=\hat{z}} = R n_r \frac{k'}{k^2}. \quad (\text{A3})$$

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

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

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

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

or, equivalently

$$\left[-R n_r \frac{\partial}{\partial z_m} \left(\frac{\alpha' k - \alpha k'}{k^2} \right) \right]_{z_m=\hat{z}=z^*} < 0. \quad (\text{A6})$$

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

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

543 and z^* is therefore evolutionary stable when

$$\alpha'' > k''/K. \quad (\text{A8})$$

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

$$\alpha'' > -1/\sigma_k^2. \quad (\text{A9})$$

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

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

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

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

548 6 Appendix B

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

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

552 Since there is no analytical solution for the indefinite integral on the left hand side, we use the
553 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
554 Taylor series about $\hat{z} - z_n^* = 0$ leads us to assume a small change in abundance and hence
555 constant mutational input μK . We therefore replace K with K_0 to indicate that mutational

556 input depends on the original abundance. We now have

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

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

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

557 Approximating to the first order

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

558 and solving for \hat{z} gives

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

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

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

560 Subbing Equation B7 into Equation 2 gives an approximate description of population abun-
561 dance across evolutionary time (Equation 8).

562 7 Appendix C

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

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

565 where z_m and n_m are the trait value and abundance of a rare mutant, respectively, in a popula-
566 tion 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

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

568 And from Equation 14:

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

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

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

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 $\alpha(z_i, z_i) = 1$:

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

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

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

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 $z_m = \hat{z} = z_c^*$,

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

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

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

581 8 Appendix D

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

$$\frac{d\hat{z}}{dt} = \frac{-\mu\sigma_\mu^2}{2} [k - C] R \left[\frac{k' - C'}{k} \right] \quad (\text{D1})$$

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

585 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
 586 when

$$\left| \frac{(k - C)(k' - C')}{k} \right| > |k'|. \quad (\text{D3})$$

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

$$|k' - C'| > \frac{k}{k - C} |k'|, \quad (\text{D4})$$

588 yielding Equation 17.

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749 9 Figure captions

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

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

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

774 Figure 4: Accuracy of analytical prediction, in the one-population case. Each point repre-
 775 sents the mean \pm SE for ten replicated simulation runs. Solid line is 1:1 line; points falling
 776 on line represent perfect predictions of time at risk t_r . Squares: $\mu K \log(K) \leq 0.1$; Circles:
 777 $\mu K \log(K) \leq 1$; 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 $\hat{z} \rightarrow z_{c,n}^*$. 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**

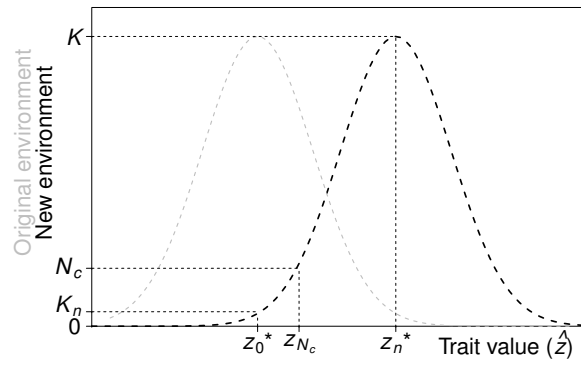


Figure 1:

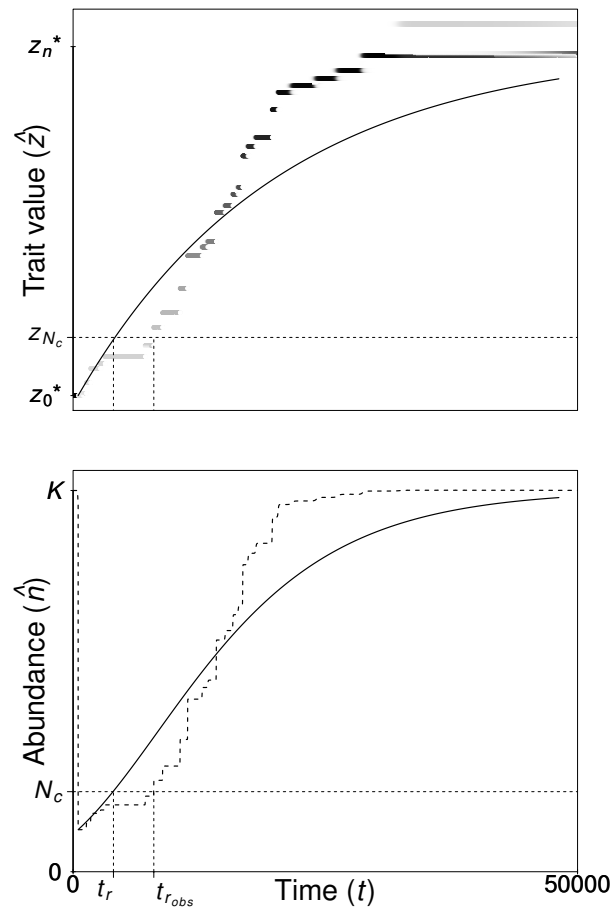


Figure 2:

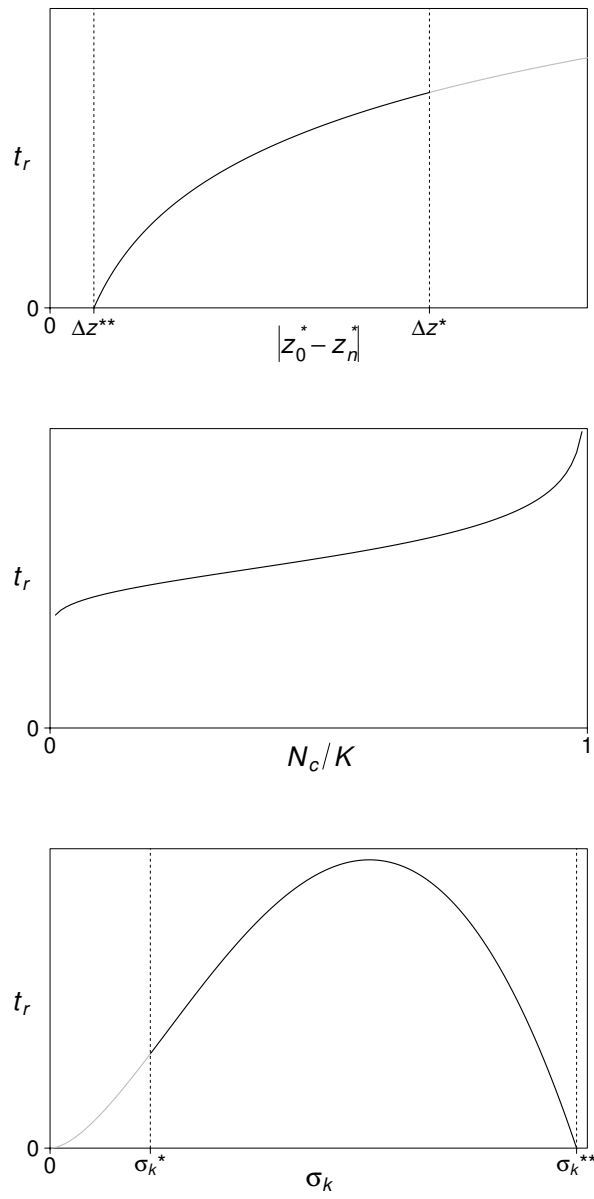


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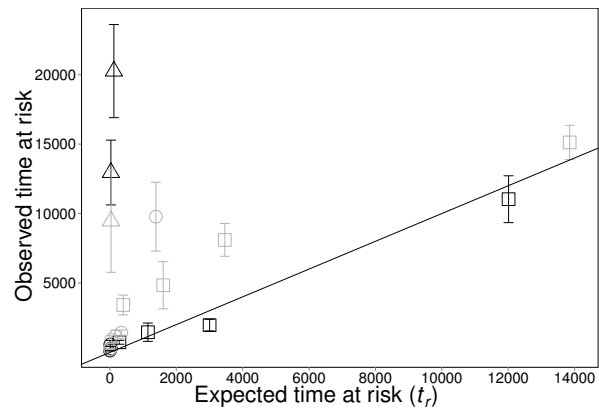


Figure 4:

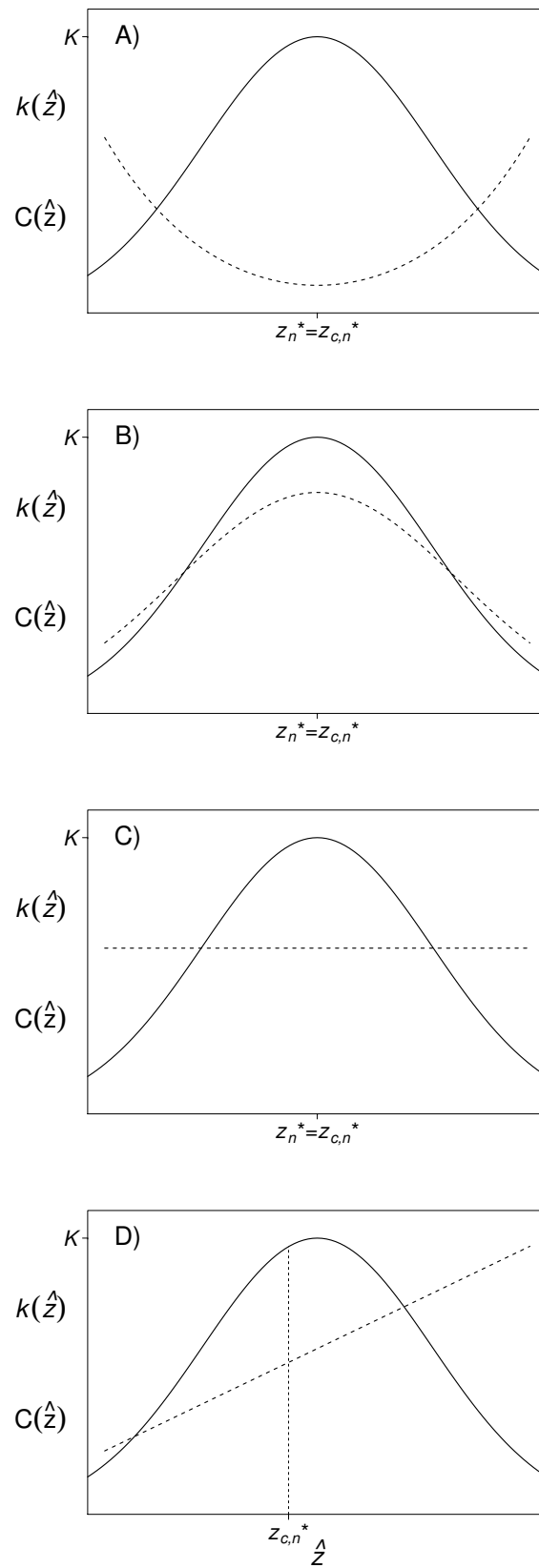


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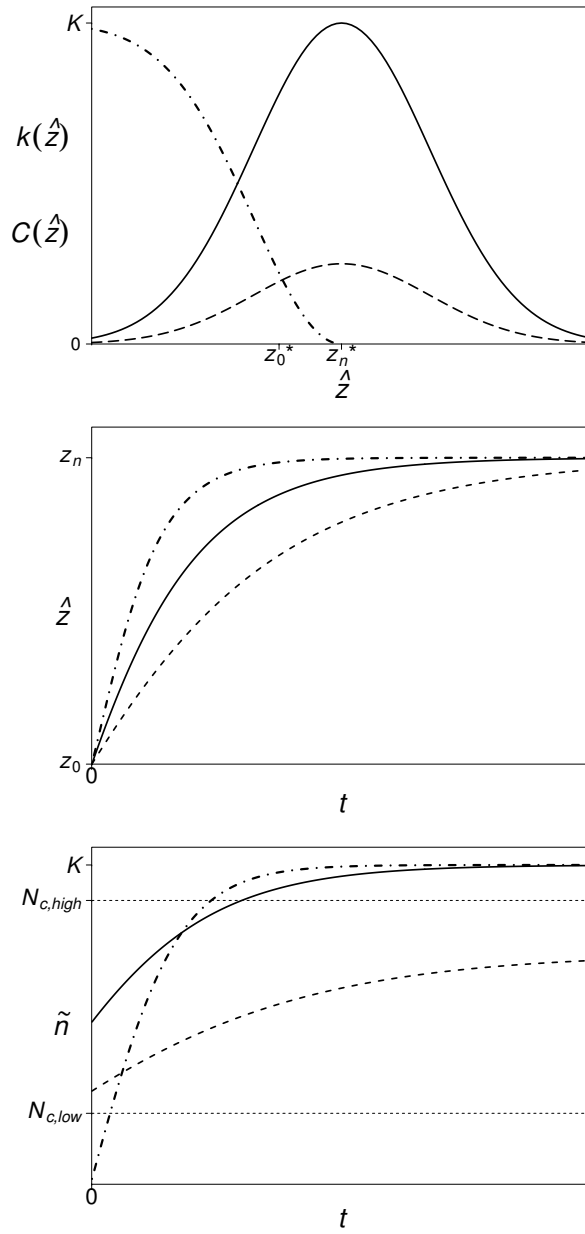


Figure 6: