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Author for correspondence:
Matthew Miles Osmond
e-mail: matthew.osmond@mail.mcgill.ca

†Present address: Station d'Ecologie Experimentale, Centre National de la Recherche Scientifique, 09200 Moulis, France.

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How competition affects evolutionary rescue

Matthew Miles Osmond and Claire de Mazancourt†

Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal, Quebec, Canada H3A 0C4

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.

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 [6–10]. A population's ability to adapt and persist in changing environments will therefore also hinge on the surrounding community [11] (see also [12]). 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 [17–20]. 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 [24–26] 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 theories on adaptation to abrupt environmental change consider only isolated populations [3,28–33], 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 continuously changing environment, by adding a selection pressure that effectively 'pushes' the more adapted populations in the direction of the moving environment [36].

Here we use the mathematical framework of adaptive dynamics to describe the evolutionary and demographic dynamics of a population experiencing competition and an abrupt change in the environment. Adaptive dynamics allows us to incorporate both intra- and interspecific competition in an evolutionary model while maintaining analytical tractability. We assess the potential for evolution to rescue populations by measuring the 'time at risk', i.e. the time a population spends below a critical abundance [3]. First, we derive an expression for the 'time at risk' in a population undergoing an abrupt change in isolation. We then compare our results to previous studies and test the robustness of our results by relaxing a number of simplifying assumptions using computer simulations. Finally, we examine how a population's ability to adapt and persist to an abrupt environmental change is impacted by the presence of competing species.

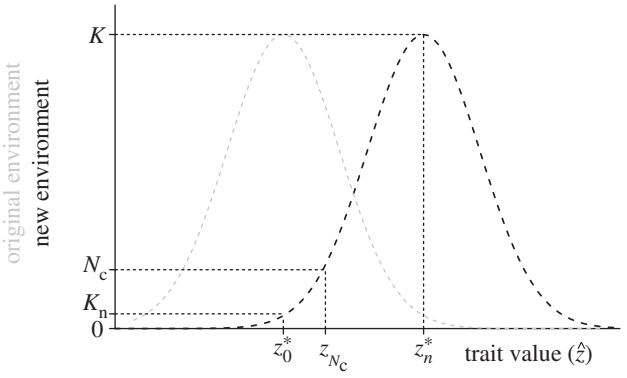

Figure 1. Our initially adapted population is monomorphic for the optimal phenotype in the original environment $\hat{z} = z_0^*$ (grey). When the environment changes, the carrying capacity function shifts (black). The new carrying capacity of our population $K_n = k(z_0^*, z_n^*)$ is the height of the 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 $\hat{z} < z_{N_c}$.

2. Model and results

(a) One-population model

We first examine how, in the absence of competitors, an asexual population with density- and frequency-dependent population growth responds to an abrupt change in the environment.

We assume that each individual in the population has a trait value z, and that a phenotype's growth rate is determined by both its own trait value as well as the trait value of all other individuals within the population. Population dynamics are described by the logistic equation (eqn 2 in [37])

$$\frac{dn_i}{dt} = n_i R\left(1 - \frac{\int \alpha(z_i, z_j) n_j \, dz_j}{k(z_i, z*)}\right), \tag{2.1}$$

where n_i is the number of individuals with trait value z_i, R is the *per capita* intrinsic growth rate, $\alpha(z_i,z_j)$ is the *per capita* competitive effect of individuals with trait z_j on individuals with trait z_i, and $k(z_i,z^*)$ is the carrying capacity of individuals with trait z_i in an environment where the trait value giving maximum carrying capacity is z^*. We describe carrying capacity k as a Gaussian distribution (eqn 1 in [37])

$$k(z_i, z^*) = K e^{-(z_i - z^*)^2/2\sigma_k^2}, \tag{2.2}$$

where K is the maximum carrying capacity and $\sigma_k > 0$ is the 'environmental tolerance', which describes how strongly carrying capacity varies with z_i. For a given deviation from z^*, smaller variances σ_k^2 mean larger declines in carrying capacity k. We therefore refer to σ_k^{-2} as the strength of stabilizing selection. Data on yeast responses to salt [5,38] fit Gaussian carrying capacity functions, as described in equation (2.2) (see the electronic supplementary material).

We do not give a specific form for intraspecific competition α, but instead give requirements that are satisfied by a wide range of functions. First, we assume that individuals with the same trait value compete most strongly, that is $(d/dz)\alpha(z,z) = 0$ and $(d^2/dz^2)\alpha(z,z) < 0$. This is biologically reasonable and could describe, for instance, the effect of beak size on finches competing for seeds, where individuals with similar-sized beaks compete strongly for similar-sized seeds [39]. And we arbitrarily set $\alpha(z,z) = 1$, meaning that individuals with the same trait value take up one 'unit' of carrying capacity.

Trait value z is assumed to be determined by a large number of loci, each with equal and small effect, making the range of possible phenotypes continuous and unbounded (i.e. $z \in \mathbb{R}$). To proceed analytically, we first assume that mutations are rare. The population remains monomorphic, with all individuals having 'resident' trait value $\hat{z}$. The evolutionary trajectory is determined by the *per capita* growth rate of rare mutants in the neighbourhood of $\hat{z}$ (adaptive dynamics; [40]). When mutations are sufficiently rare, evolution occurs slowly enough for us to consider the population at demographic equilibrium on an evolutionary time-scale. This stands in contrast with previous models which jointly model demography and evolution [3,34]. The time-scale separation between demography and evolution allows us to incorporate intra- and interspecific competition while maintaining analytical tractability. We later use computer simulations to examine how our analytical results perform when demography and evolution occur on similar time-scales.

In appendix A, we show that when $(d^2/dz^2)\alpha(z,z) > \sigma_k^{-2}$ the 'optimal trait value' z^* is both convergence stable (i.e. by small steps the resident trait converges to z^*) and evolutionarily stable (i.e. once $\hat{z} = z^*$ no other strategies can invade; z^* is an ESS, *sensu* Maynard Smith & Price [41]). We assume $(d^2/dz^2)\alpha(z,z) > \sigma_k^{-2}$ for the remainder of the paper, which means frequency-dependence is weak enough [42]. Our results apply for any function α, as long as z^* is both convergence and evolutionarily stable.

Let our population begin in a constant environment with optimal trait value $z^* = z_0^*$. In time, all individuals become perfectly adapted $\hat{z} = z_0^*$. The population will reach equilibrium abundance $\tilde{n} = K$, and its growth rate will become zero (figure 1). Let us call this original abundance K_0.

Suppose then that the environment suddenly changes so that the new optimal trait value is $z_n^* \neq z_0^*$. Our monomorphic population, with trait value $\hat{z} = z_0^*$, then immediately has equilibrial abundance $k(z_0^*, z_n^*) < K_0$ (figure 1). The

environmental change serves to decrease the carrying capacity of the population. The population will initially survive the abrupt change if $k(z_0^*, z_n^*) \geq 1$ or, equivalently

$$|z_0^* - z_n^*| \leq \sigma_k \sqrt{2\ln(K)} \equiv \triangle z^*. \tag{2.3}$$

Note that setting $\tilde{n} \geq 1$ as the extinction threshold scales population abundance in units of minimal viable population size [37,43]. Because z_n^* is the new evolutionarily and convergence stable strategy, if the population survives the change it will evolve towards the new optimal trait value, $\hat{z} \to z_n^*$. According to the canonical equation of adaptive dynamics [44], the monomorphic trait value $\hat{z}$ will change at rate

$$\frac{d\hat{z}}{dt} = \frac{\mu\sigma_\mu^2}{2}\tilde{n}(\hat{z}, z_n^*)g(\hat{z}, z_n^*), \tag{2.4}$$

where μ is the *per capita* per generation mutation rate, σ_μ^2 is the mutational variance (mutations symmetrically distributed with mean of parental value) and $g(\hat{z}, z_n^*)$ is the local fitness gradient (appendix A):

$$g(\hat{z}, z_n^*) = \frac{\partial}{\partial z_m}\left(\frac{1}{n_m}\frac{dn_m}{dt}\right)\Bigg|_{z_m=\hat{z}} = \frac{-R(\hat{z} - z_n^*)}{\sigma_k^2}, \tag{2.5}$$

where n_m and z_m are a rare mutant's abundance and trait value, respectively, and $\hat{z}$ is the resident trait value [40]. The local fitness gradient describes the slope of the fitness function in the neighbourhood of the parental trait value. Steeper slopes signify greater fitness differences between individuals with similar but unequal trait values [45]. Notice that R/σ_k^2 is the strength of stabilizing selection per unit time.

The rate of change in trait value is then

$$\frac{d\hat{z}}{dt} = -\frac{\mu\sigma_\mu^2 R(\hat{z} - z_n^*)}{2\sigma_k^2} K e^{-(\hat{z}-z_n^*)^2/2\sigma_k^2}. \tag{2.6}$$

We cannot solve equation (2.6) explicitly for $\hat{z}(t)$, but using a first-order Taylor expansion, we derive an approximate solution, describing evolution and demography following the abrupt change (appendix B):

$$\hat{z}(t) \approx z_n^* + (z_0^* - z_n^*) e^{(-\mu\sigma_\mu^2 K_0 R/2\sigma_k^2)t} \tag{2.7}$$

and

$$\tilde{n}(t) \approx K \exp\left[\frac{-((z_0^* - z_n^*) e^{(-\mu\sigma_\mu^2 K_0 R/2\sigma_k^2)t})^2}{2\sigma_k^2}\right]. \tag{2.8}$$

Taking the Taylor expansion about $z_0^* - z_n^* = 0$ results in the assumption that the environmental change $|z_0^* - z_n^*|$ is small relative to environmental tolerance α_k (i.e. a weak 'initial stress'). Our first-order approximation of the Gaussian k is therefore taken at the maximum $z = 0$, which is a line with slope zero and height K_0. This means we assume mutational input μk is constant at μK_0, effectively decoupling the demographic and evolutionary dynamics of the recovering population. Our first-order approximation is the highest-order for which we can obtain an analytical solution.

Now, let N_c be the abundance below which demographic or environmental stochasticity are likely to cause rapid extinction [3,46]. We use this heuristic N_c, in the place of stochastic models, for simplicity. We are interested in the amount of time a population spends below this threshold, i.e. how long the population is at risk of extinction.

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

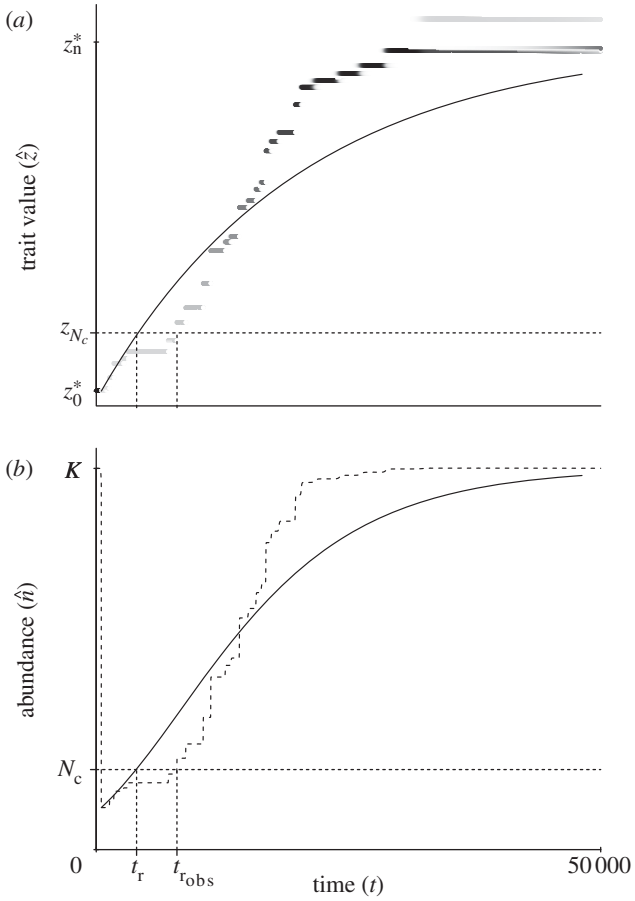

Figure 2. Adaptation following an abrupt change in the environment. (*a*) Population trait value $\hat{z}$ evolves towards the new optimal z_n^* (equation (2.7)). The time it takes to evolve a trait value z_{N_c}, which gives a critical abundance N_c, is the expected 'time at risk' t_r (equation (2.10)). (*b*) Population abundance $\tilde{n}$ increases as the population adapts to the new environment (equation (2.8)). Solid lines are analytical predictions (equations (2.7) and (2.8)). 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 $t_{r_{obs}}$.

N_c. In this model, equilibrial abundance strictly increases in evolutionary 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,

$$|z_0^* - z_n^*| < \sigma_k \sqrt{2\ln\left(\frac{K}{N_c}\right)} \equiv \triangle z^{**}. \tag{2.9}$$

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 (2.2), we can find the trait value z_{N_c} required for a carrying capacity of N_c. Plugging z_{N_c} into equation (2.7) 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)

$$t_r = \frac{\sigma_k^2}{\mu\sigma_\mu^2 K_0 R}\ln\left[\frac{(z_0^* - z_n^*)^2}{2\sigma_k^2\ln(K/N_c)}\right]. \tag{2.10}$$

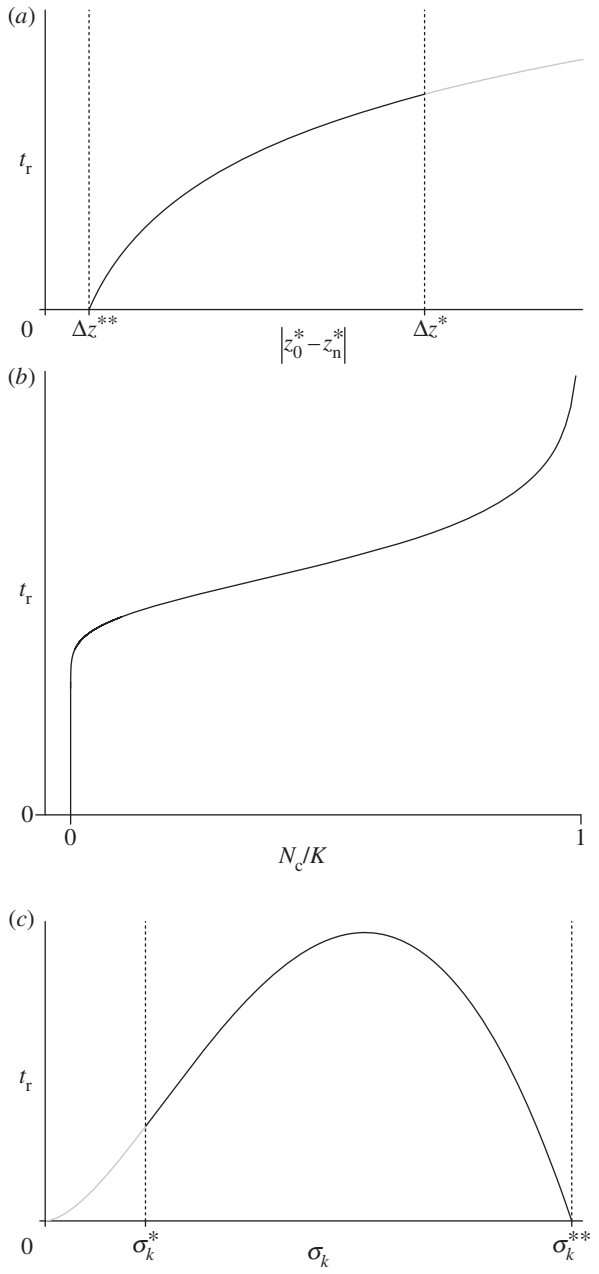

Figure 3. (*a*) Time at risk t_r (equation (2.10)) increases monotonically with the magnitude of environmental change $|z_0^* - z_n^*|$. Magnitudes of change smaller than Δz^{**} are not large enough to put the population at risk of extinction (equation (2.9)) and magnitudes of change larger than Δz^* cause immediate extinction (equation (2.3)). (*b*) Time at risk t_r increases as the critical abundance N_c approaches maximum abundance K. As the critical abundance approaches the maximum abundance, $N_c/K \longrightarrow 1$, the ratio has a stronger effect on the time at risk. (*c*) 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 (2.3) and (2.9), respectively).

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.

(b) Comparison of one-population model to previous work

Here, we compare our one-population model to previous discrete-time quantitative genetic models [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 & Holt [3] describe the evolutionary trajectory of the population mean trait value as a geometrical approach to the optimum (eqn 5 in [3]):

$$d_t = d_0 \left[\frac{w + (1 - h^2)P}{w + P}\right]^t, \tag{2.11}$$

where d_t is the distance of the population mean trait value from the trait value giving maximum growth rate at time t, w is the variance of the growth rate function, h^2 is the trait heritability and P is the constant phenotypic variance [3]. We derive a qualitatively similar trajectory (equation (2.7)), in continuous time, from adaptive dynamics. Adaptive dynamics provides greater ecological context by including intrinsic growth rate and maximum carrying capacity as parameters in the evolutionary trajectory. The trajectories are identical when

$$\frac{w + (1 - h^2)P}{w + P} = \exp\left[\frac{-\mu\sigma_\mu^2 K_0 R}{2\sigma_k^2}\right]. \tag{2.12}$$

Gomulkiewicz & Holt [3] refer to equation (2.12) as the evolutionary 'inertia' of a trait. Inertia is bounded between zero and unity in both models. When inertia is unity there is no evolution. In Gomulkiewicz & Holt [3], evolution halts when trait heritability h^2 or phenotypic variance P is zero. In our model, inertia is determined by mutational input μK_0, and evolution halts when there are no mutations. For a given w and $h^2 \neq 0$, inertia is minimized and evolution proceeds at a maximum rate in Gomulkiewicz & Holt [3] as phenotypic variance goes to infinity $P \rightarrow \infty$. In our model, for a given strength of stabilizing selection per unit time R/σ_k^2, inertia approaches zero and the rate of evolution is maximized as mutational input goes to infinity $\mu K_0 \rightarrow \infty$.

Note that to maintain analytical tractability both models assume the material which selection acts upon (phenotypic variance P or mutational input μK_0) is constant. Both models will therefore be more accurate when the environmental change is relatively small. Large changes in the environment are likely to cause strong selection and large variation in abundance, which could greatly alter phenotypic variance and mutational input [30]. Since phenotypic variance and mutational input are expected to decline under strong stabilizing selection and reduced abundance [47], respectively, the analytical results of both models will tend to underestimate a population's time at risk.

Our evolutionary trajectory aligns even more closely with that of Chevin and Lande (eqn 10 in [34]; also see eqn 18a in [48]), who incorporated both density-dependence and phenotypic plasticity. The two trajectories are identical when there is constant plasticity $\varphi = 0$, additive genetic variance is equivalent to the supply rate of beneficial

mutations multiplied by mutational size $\sigma_a^2 = \mu\sigma_\mu^2 K_0/2$, and the two measures of stabilizing selection strength per unit time are the same $\gamma^* = R/\sigma_k^2$.

Although our evolutionary trajectory aligns closely with those of Gomulkiewicz & Holt [3] and Chevin & Lande [34], we uncover an analytical approximation for the time at risk t_r by assuming a time-scale separation between demographics and evolution. Gomulkiewicz & Holt [3] and Chevin & Lande [34] do not assume such a time-scale separation, leading to more complex population dynamics and the need to calculate t_r numerically. This makes a quantitative comparison with our time at risk approximation impossible. However, Gomulkiewicz & Holt [3] agree that the time at risk t_r should increase with initial maladaptation (i.e. magnitude of environmental change) $|z_0^* - z_n^*|$ and that at high degrees of maladaptation the relationship with time at risk should be close to linear (figure 3; fig. 5A in [3]). In addition, in both Gomulkiewicz & Holt [3] and Chevin & Lande [34] strengthening selection $1/\omega \to \infty$ increases the rate of adaptation while decreasing abundance (through a decline in mean fitness). Time at risk should therefore be minimized at an intermediate selection strength, as in our model (figure 3*c*), although they do not explore this explicitly. Gomulkiewicz & Holt [3] also argue that the time at risk t_r should decrease with the abundance before environmental change, since the population declines geometrically beginning at this abundance. In our model, time at risk also decreases with abundance before environmental change K_0, but for a different reason. Recall that because of our first-order approximation we assume a small initial stress and hence a small change in abundance. This allows us to assume that mutations are supplied at a constant rate μK_0, where μ is the *per capita* mutation rate and K_0 is the abundance before environmental change. A greater abundance before environmental change K_0 therefore causes faster evolution resulting in less time at risk.

(c) Simulations

Adaptive dynamics assumes mutations are rare enough such that, on the time-scale 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 (2.10)) 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 (i) mutation rate μ and maximum carrying capacity K, (ii) mutational variance σ_μ^2, and (iii) 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 (2.1), using a fourth-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 unity 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 time-step 500, the optimal trait value instantaneously shifted to $z_n^* \neq z_0^*$. Simulations were terminated at time-step 50 000. Code available upon request; implemented in R [50].

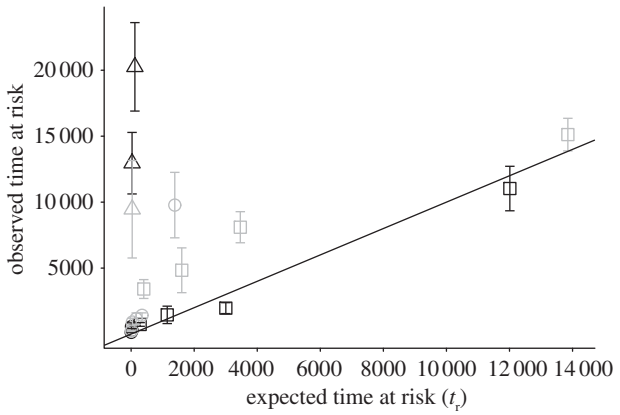

Figure 4. Accuracy of analytical prediction, in the one-population case. Each point represents the mean ± s.e. for 10 replicated simulation runs. Solid line is 1 : 1 line; points falling on line represent perfect predictions of time at risk t_r. Squares, $\mu K \log(K) \leq 0.1$; circles, $\mu K \log(K) \leq 1$; triangles, $\mu K \log(K) > 1$; black, $|z_0^* - z_n^*|\sigma_k^{-1} = 1.2$; grey, $|z_0^* - z_n^*|\sigma_k^{-1} = 2.1$. Parameters: $\mu = \{10^{-7}, 10^{-6}, 10^{-5}, 10^{-4}\}$, $K = \{10^4, 10^5, 10^6\}$, $\sigma_\mu = \{0.01, 0.05\}$, $R = 1$, $\sigma_k = 1$, $\sigma_\alpha = 1.5$ and N_c is 1000 greater than the minimum abundance of each run.

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 fig. S1 in Bell & Gonzalez [5] (see the electronic supplementary material).

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 prediction (equations (2.7) and (2.8); figure 4). In simulations, the amount of standing phenotypic variance increases with mutation rate μ multiplied by population size. Our time-scale assumption, which implies zero phenotypic variance, is thought to become unrealistic as $\mu K \log(K)$ approaches unity [51]. The threshold of $\mu K \log(K)$ is obtained because μK is the mutational input and $\log(K)$ is the typical time of fixation for a successful mutant when the population is well adapted [51]. Over our parameter range ($\mu = \{10^{-7}, 10^{-6}, 10^{-5}, 10^{-4}\}$, $K = \{10^4, 10^5, 10^6\}$) $\mu K \log(K)$ seemed to be an excellent predictor of accuracy; our predictions were much more accurate when $\mu K \log(K) < 1$. When $\mu K \log(K) > 1$, we greatly underestimated the time at risk (triangles in figure 4).

Mutational variance σ_μ^2 seemed to have little effect on the accuracy of our predictions, at least over the range of parameter space explored here ($\sigma_\mu = \{0.01, 0.05\}$; figure 4). However, our analytical prediction did perform consistently better when the initial stress $|z_0^* - z_n^*|\sigma_k^{-1}$ was small, for all parameter combinations (compare black $|z_0^* - z_n^*|\sigma_k^{-1} = 1.2$ and grey $|z_0^* - z_n^*|\sigma_k^{-1} = 2.1$ points in figure 4).

(d) Competition

We now introduce interspecific competition. Let the population dynamics of the focal population be described by the logistic growth equation

$$\frac{\mathrm{d}n_i}{\mathrm{d}t} = n_i R\left(1 - \frac{\int \alpha(z_i, z_j) n_j \,\mathrm{d}z_j + C(z_i, t)}{k(z_i, z^*)}\right), \tag{2.13}$$

where $C(z_i,t) \geq 0$ is the effect of interspecific competition on individuals in the focal population with trait value z_i at time t. We do not model the coevolution of the competitors explicitly; we instead keep interspecific competition $C(z_i,t)$ as general as possible, allowing it to depend on focal trait value z_i and vary in time t with any other biotic or abiotic factor (including the trait values and abundance of the focal and competing populations). For evolutionary rescue of the focal population, the only relevant dependency is with z_i. Our formulation allows competition C to encompass all possible types of coevolution feedback. In fact, C could even be interpreted as an abiotic selection pressure. However, for brevity, we limit our discussion to C as the effect of a competitor. Previous studies have explicitly modelled the coevolution of competing species in a constant environment [37,52,53], at the expense of analytical results. All other variables in equation (2.13) are defined as in the one-population case.

We again assume that mutations are rare, so that our focal population remains monomorphic with trait value $\hat{z}$ and equilibrial abundance $\tilde{n}$. In the presence of competition, equilibrium abundance of the focal population is

$$\tilde{n}(\hat{z}, z^*, t) = k(\hat{z}, z^*) - C(\hat{z}, t). \tag{2.14}$$

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

Now, let the competing populations coexist in a constant environment with $z^* = z_0^*$. The equilibrial abundance ñ of the focal population is not necessarily maximized at z_0^*, but at a 'competitive optimal' $z_{\mathrm{c},0}^*$ (appendix C). Assuming $z_{\mathrm{c},0}^*$ is a fitness maximum (appendix C), the focal population will eventually evolve to the competitive optimal $\hat{z} = z_{\mathrm{c},0}^*$. We then let the competitive optimal change abruptly, to new trait value $z_{\mathrm{c,n}}^* \neq z_{\mathrm{c},0}^*$. This change could arise from a shift in competition C or in the optimal trait value $z^* = z_{\mathrm{n}}^*$. The abundance of the focal population is now $k(z_{\mathrm{c},0}^*, z_{\mathrm{n}}^*) - C(z_{\mathrm{c},0}^*, t)$. The amount of competition a population feels immediately following the environmental change $C(z_{\mathrm{c},0}^*, t)$ will depend on the type of environmental change as well as the response of the competitors. Competition may be close to negligible if resources remain plentiful but the abundance of competitors are greatly reduced (e.g. when a pollutant causes severe mortality in the competitor). However, competition may be exceptionally strong if the change in environment is a shift in available resources, so that the supply of resources is limiting (e.g. seed size changes on an island supporting multiple species of finch [54]). Persistence requires $k(z_{\mathrm{c},0}^*, z_{\mathrm{n}}^*) - C(z_{\mathrm{c},0}^*, t) \geq 1$, and therefore persistence following environmental change is more likely when competition $C(z_{\mathrm{c},0}^*, t)$ is weak.

In appendix C, we derive the local fitness gradient of the focal population. In the new environment, with $z^* = z_{\mathrm{n}}^*$, it can be written as

$$g(\hat{z}, z_{\mathrm{n}}^*, t) = \frac{\partial}{\partial z_{\mathrm{m}}}\left(\frac{1}{n_{\mathrm{m}}}\frac{\mathrm{d}n_{\mathrm{m}}}{\mathrm{d}t}\right)\Bigg|_{z_{\mathrm{m}}=\hat{z}} = R\left[\frac{(\partial/\mathrm{d}\hat{z})(k(\hat{z}, z_{\mathrm{n}}^*) - C(\hat{z}, t))}{k(\hat{z}, z_{\mathrm{n}}^*)}\right]. \tag{2.15}$$

The population evolves in a direction that increases abundance $k - C$ until $(\partial/\partial\hat{z})(k - C) = 0$, which occurs when the population reaches the competitive optimal in the new environment $\hat{z} = z_{\mathrm{c,n}}^*$ (figure 5). We assume that $z_{\mathrm{c,n}}^*$ is a fitness maximum, such that the population remains monomorphic (appendix C).

From equation (2.15) we see that, relative to the one-population case (equation (2.5)), 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 $|(\partial/\partial\hat{z})(k - C)| > |(\partial/\partial\hat{z})k|$. This is will always occur when competition selects in the same direction as carrying capacity (i.e. $\partial k/\partial\hat{z}$ and $\partial C/\partial\hat{z}$ are of different signs). Competition decreases selection when $|(\partial/\partial\hat{z})(k - C)| < |(\partial/\partial\hat{z})k|$, which will occur when competition weakly selects in the opposite direction to carrying capacity (i.e. $\partial k/\partial\hat{z}$ and $\partial C/\partial\hat{z}$ are of the same sign and $|\partial C/\partial\hat{z}|$ is small). When competition selects in the opposite direction as carrying capacity and has a stronger selective effect $|\partial C/\partial\hat{z}| > |\partial k/\partial\hat{z}|$, 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 $\partial C/\partial\hat{z} = 0$.

Combining equations (2.14) and (2.15), we compute the rate of adaptation, as described by the canonical equation [44]:

$$\frac{\mathrm{d}\hat{z}}{\mathrm{d}t} = \frac{-\mu\sigma_\mu^2}{2}[k(\hat{z}, z_{\mathrm{n}}^*) - C(\hat{z}, t)]R\left[\frac{(\partial/\mathrm{d}\hat{z})(k(\hat{z}, z_{\mathrm{n}}^*) - C(\hat{z}, t))}{k(\hat{z}, z_{\mathrm{n}}^*)}\right]. \tag{2.16}$$

The rate the focal population adapts $\mathrm{d}\hat{z}/\mathrm{d}t$ depends on how competition affects abundance relative to selection. Owing to the added complexity of competition we are unable to solve equation (2.16) 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 (2.16) and comparing with the one-population case (equation (2.6)) show that competition will increase the rate of adaptation when (appendix D)

$$\left|\frac{\partial}{\partial\hat{z}}(k(\hat{z}, z_{\mathrm{n}}^*) - C(\hat{z}, t))\right| > \frac{k(\hat{z}, z_{\mathrm{n}}^*)}{k(\hat{z}, z_{\mathrm{n}}^*) - C(\hat{z}, t)}\left|\frac{\partial k(\hat{z}, z_{\mathrm{n}}^*)}{\partial\hat{z}}\right|, \tag{2.17}$$

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 $z_{\mathrm{c,n}}^*$ (dotted-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} (figure 6*c*). As maximal abundance $[k - C]\hat{z} = z_{\mathrm{c,n}}^*$ approaches the critical value N_{c} evolutionary rescue becomes

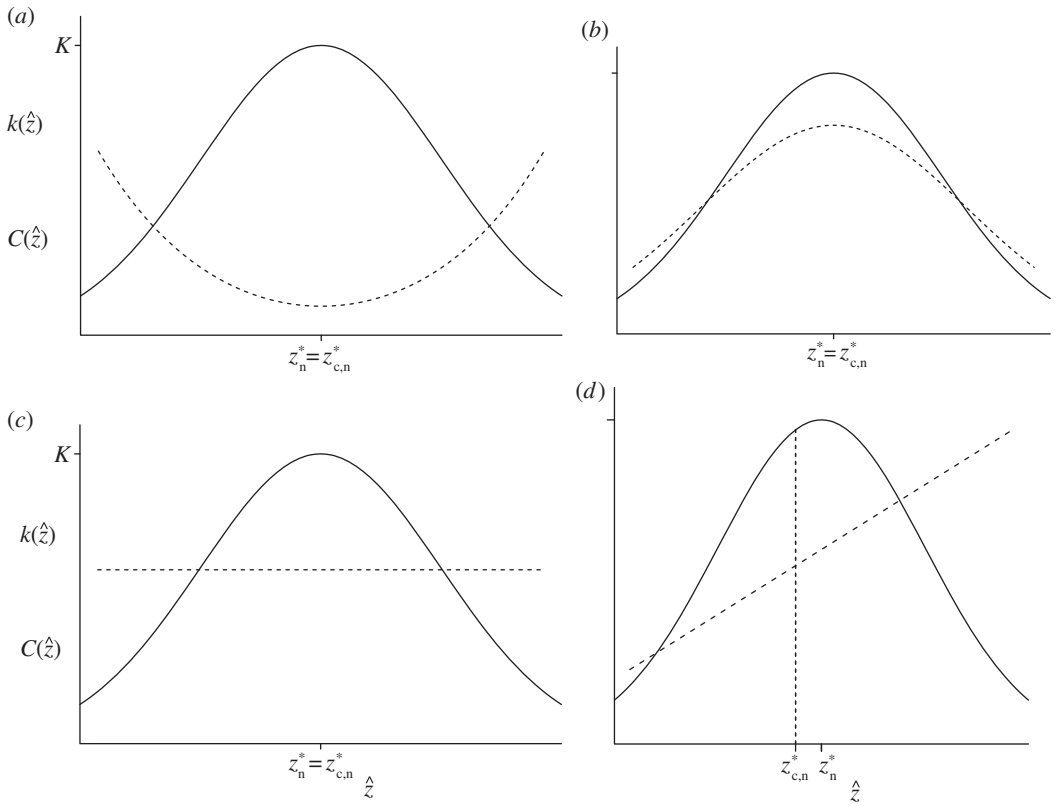

Figure 5. Selection pressures from carrying capacity and competition. The population evolves in the direction which increases abundance according to equation (2.15). Population size is carrying capacity minus competition $k - C$ (solid curve minus dashed curve). Populations can persist in communities only when they have positive population size (region of persistence; solid line higher than the dashed line). The selection pressure in the new environment is proportional to the selection for carrying capacity (slope of solid curve) minus the selection for competition (slope of dashed curve). The population will therefore evolve towards the trait value for which the slopes of the two curves are equal $\hat{z} \longrightarrow z^*_{c,n}$. The effective selection pressure will depend on the shape of the two curves and the position of the population in trait space. (*a*) Competition increases selection pressure. Competition decreases as carrying capacity increases, meaning both carrying capacity and competition select in the same direction. (*b*) Competition reduces selection pressure. Competition increases as carrying capacity increases, meaning carrying capacity and competition exert opposing selection pressures. Note that if the competition curve was steeper than carrying capacity competition could reverse the direction of evolution. (*c*) Competition affects all phenotypes equally, and therefore has no effect on selection pressure. (*d*) Competition increases or decreases selection pressure. When $\hat{z} < z^*_{c,n}$ competition and carrying capacity exert opposing selection pressures. When $\hat{z} > z^*_n$ competition and carrying capacity select in the same direction, towards z^*_n.

less likely, and regardless of the rate of adaptation, when $[k - C]\hat{z} = z^*_{c,n} \leq N_c$ evolutionary rescue is impossible.

3. Discussion

In nature, population abundance cannot increase indefinitely [55]. One of the main 'checks of increase' [56] is competition for resources [17,19,57–59]. 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 [44,60], 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 recent analytical work has come to a different conclusion, showing that, relative to the density-independent case, density-dependence can increase the rate at which abundance declines as well as decrease the rate abundance recovers, therefore increasing the time a population spends at risk of extinction [34]. The conflicting results are due to the different types of density-dependence used in the two studies. In Boulding & Hay [29], density-dependence is linear (i.e. *per capita* growth rate declines linearly with abundance) while in Chevin & Lande [34] density-dependence is stronger than linear at low abundances (the *per capita* growth rate declines logarithmically with abundance). Since it is the effect of density-dependence at low abundances that is critical for population persistence, this explains why Chevin & Lande [34] claim density-dependence increases the chances of extinction. A similar trend is expected in biological invasions, where populations experiencing strong density-dependence at low abundances are predicted to invade slowly [64].

Here we assume evolution is slow, and hence, on the timescale of evolution, populations are always at carrying capacity. Carrying capacity therefore indicates how well a population is adapted; populations below carrying capacity will increase in abundance without evolving, and hence may not require evolutionary rescue if their carrying capacity is large enough. In our model, it is the *maximum* carrying capacity that affects the

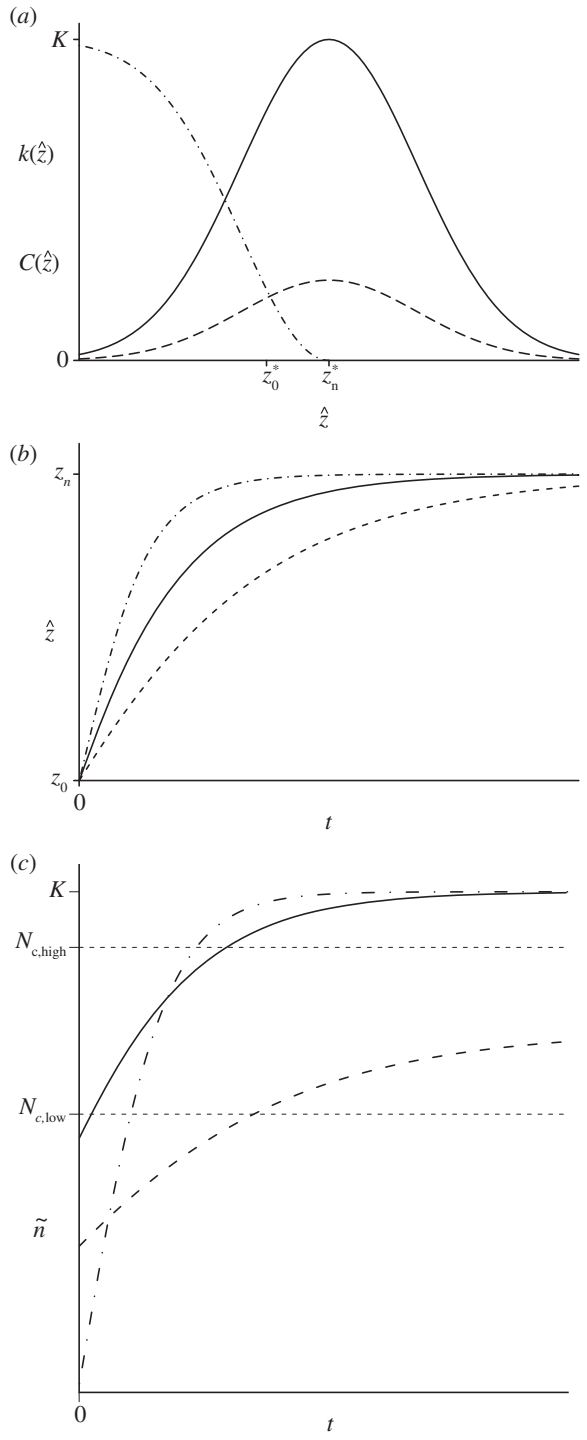

Figure 6. Competition can help or hinder evolutionary rescue. (*a*) Carrying capacity k (solid curve) as a function of trait value $\hat{z}$ and two competition C scenarios: complete niche overlap (dashed curve) or partial niche overlap (dotted-dashed curve). (*b*) With complete niche overlap (dashed curve) competition increases as the population adapts, and the population therefore adapts slower than it would without competition (solid curve). With partial niche overlap (dot-dashed curve) competition decreases as the population adapts, and the population adapts faster. (*c*) The time a population spends at risk of extinction (the time abundance $\tilde{n}$ is below critical abundance N_c) depends on competition's effect on abundance and evolution as well as on the value of the critical abundance. For instance, when the critical abundance is low $N_{c,low}$ both competition scenarios increase the time at risk relative to when there is no competition (solid curve) because they depress the focal population's abundance. However, when the critical abundance is high $N_{c,high}$ partial niche overlap (dotted-dashed curve) decreases the time at risk relative to the no competition case (solid curve) because it sufficiently increases the rate of adaptation.

potential, and need, for evolutionary rescue. Since abundance asymptotically approaches maximum carrying capacity in evolutionary time (figure 2), maximum carrying capacity will have a larger effect on the time at risk as it approaches the critical abundance (figure 3).

Notice that maximum carrying capacity plays both a demographic and evolutionary role; for a given environmental change, larger values keep populations at larger abundances (K in equation (2.8)) and, following the change, increase the rate of evolution (K_0 in equation (2.7)). Here we assume greater abundances lead to faster evolution because they cause greater mutational inputs. In previous models [3,34], where the rate of evolution is determined by additive genetic variation instead of mutational input, the relationship between population size and the rate of evolution can be weaker (reviewed in [65]). Although non-additive genetic effects, such as epistasis and dominance, and temporal fluctuations in abundance (leading to lower effective population sizes) can weaken the relationship between population size and the rate of evolution [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 [3,34]. We derive a similar evolutionary trajectory and agree with Gomulkiewicz & Holt [3] on 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 equal 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 probably arises from the adaptive dynamic assumption that fixation occurs instantaneously and the population remains monomorphic. In simulations that 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 referred 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 fewer.

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 [3,48]) 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 [62,70]. 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 towards 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 to which the focal population is attempting to adapt. 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 to which the focal population is attempting to adapt, it can speed adaptation by depressing the fitness of individuals in the focal population which are farther from the new niche (dotted-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, possibly 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 (2.10)) 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. In doing so, we have highlighted the general ecological and evolutionary settings where competition should help or hinder persistence to environmental change.

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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 (2.1), the local fitness gradient is

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

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 $\partial/\partial z_m$ with prime gives

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

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

$$\left.\frac{\partial}{\partial z_m}\left(\frac{1}{n_m}\frac{dn_m}{dt}\right)\right|_{z_m=\hat{z}} = Rn_r\frac{k'}{k^2}. \tag{A 3}$$

Specifying k as a Gaussian function (equation (2.2)) with mean z^* and variance σ_k^2,

$$\left.\frac{\partial}{\partial z_m}\left(\frac{1}{n_m}\frac{dn_m}{dt}\right)\right|_{z_m=\hat{z}} = -R\frac{(\hat{z}-z^*)}{\sigma_k^2}. \tag{A 4}$$

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 evolutionarily 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

$$\left.\frac{\partial^2}{\partial z_m^2}\left(\frac{1}{n_m}\frac{dn_m}{dt}\right)\right|_{z_m=\hat{z}=z^*} < 0 \tag{A 5}$$

or, equivalently

$$\left[-Rn_r\frac{\partial}{\partial z_m}\left(\frac{\alpha' k-\alpha k'}{k^2}\right)\right]_{z_m=\hat{z}=z^*} < 0. \tag{A 6}$$

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

$$-R\left(\alpha''-\frac{k''}{K}\right) < 0, \tag{A 7}$$

and z^* is therefore evolutionarily stable when

$$\alpha'' > \frac{k''}{K}. \tag{A 8}$$

Specifying k as equation (2.2), z^* is evolutionarily stable when

$$\alpha'' > -\frac{1}{\sigma_k^2}. \tag{A 9}$$

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

$$\left[\frac{\partial^2}{\partial z_m^2}\left(\frac{1}{n_m}\frac{dn_m}{dt}\right)\right]_{z_m=\hat{z}=z^*} < \left[\frac{\partial^2}{\partial \hat{z}^2}\left(\frac{1}{n_m}\frac{dn_m}{dt}\right)\right]_{z_m=\hat{z}=z^*} \tag{A 10}$$

and

$$-R\left(\alpha''-\frac{k''}{K}\right) < 0, \tag{A 11}$$

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

Appendix B

Here we derive approximations for the ecological and evolutionary dynamics in the one-population case (equations (2.7) and (2.8)). We first move all terms of equation (2.6) with $\hat{z}$ to the left-hand side and bring dt to the right. Then

taking the integral,

$$\int \frac{e^{(\hat{z}-z_n^*)^2/2\sigma_k^2}}{(\hat{z}-z_n^*)}\,d\hat{z} = \int \frac{-\mu\sigma_\mu^2 KR}{2\sigma_k^2}\,dt. \tag{B 1}$$

Since there is no analytical solution for the indefinite integral on the left-hand side, we use the Taylor expansion about $x = 0$, $e^{x^2/a}/x = \sum(x^{2n-1}/n!a^n)$, 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

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

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

and

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

Approximating to the first-order

$$\ln(\hat{z}-z_n^*) + C \approx \frac{-\mu\sigma_\mu^2 K_0 R}{2\sigma_k^2}t, \tag{B 5}$$

and solving for $\hat{z}$ gives

$$\hat{z} \approx z_n^* + e^{(-\mu\sigma_\mu^2 K_0 R/2\sigma_k^2)t - C}. \tag{B 6}$$

At $t = 0$, we have $\hat{z} = z_0^*$, so $C = -ln(z_0^* - z_n^*)$ and we get equation (2.7):

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

Subbing equation (B7) into equation (2.2) gives an approximate description of population abundance across evolutionary time (equation (2.8)).

Appendix C

Here we find the singular strategies for a population experiencing interspecific competition and evaluate their stability. From equation (2.13), the local fitness gradient is

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

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 denote $\partial/\partial z_m$ with prime. Expanding gives

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

And from equation (2.14):

$$\frac{\partial}{\partial z_m}\left(\frac{1}{n_m}\frac{dn_m}{dt}\right)\bigg|_{z_m=\hat{z}} = -R\left[(k-C)\frac{\alpha'k - \alpha k'}{k^2} + \frac{C'k - Ck'}{k^2}\right]_{z_m=\hat{z}}. \tag{C 3}$$

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

$$\frac{\partial}{\partial z_m}\left(\frac{1}{n_m}\frac{dn_m}{dt}\right)\bigg|_{z_m=\hat{z}} = R\left[\frac{\alpha'k^2 - \alpha kk' - \alpha' Ck + \alpha Ck' + C'k - Ck'}{k^2}\right]. \tag{C 4}$$

Assuming intraspecific competition α is maximal when individuals share the same trait value, $(\partial/\partial z_i)\alpha(z_i,z_i) = 0$, and $\alpha(z_i,z_i) = 1$:

$$g(\hat{z},z^*) = \frac{\partial}{\partial z_m}\left(\frac{1}{n_m}\frac{dn_m}{dt}\right)\bigg|_{z_m=\hat{z}} = -R\left[\frac{k'-C'}{k}\right]. \tag{C 5}$$

Equation (C5) determines the direction of selection. Evolution proceeds until $g(\hat{z},z^*) = 0$, in this case when $k' = C'$. The trait values giving $g(\hat{z},z^*) = 0$ are evolutionarily singular strategies, which we will denote z_c^*. If z_c^* maximizes $g(\hat{z},z^*)$, z_c^* is a fitness maximum; when $\hat{z} = z_c^*$ no nearby mutant can invade and the population remains monomorphic with $\hat{z} = z_c^*$. However, when z_c^* minimizes $g(\hat{z},z^*)$, z_c^* is a fitness minima and evolutionary branching may occur [40]. A singular point z_c^* is a fitness maximum when

$$\frac{\partial^2}{\partial z_m^2}\left(\frac{1}{n_m}\frac{dn_m}{dt}\right)\bigg|_{z_m=\hat{z}=z_c^*} = -R\left[\frac{\alpha''(k^2 - Ck) + k(C'' - k'') + (k')^2(k^3 - Ck^2 - 1)}{k^2}\right] < 0. \tag{C 6}$$

To simplify our analysis of evolutionary rescue, we assume that all singular strategies our population approaches are fitness maxima. This assumes, at $z_m = \hat{z} = z_c^*$,

$$\alpha''(k^2 - Ck) + k(C'' - k'') + (k')^2(k^3 - Ck^2 - 1) > 0. \tag{C 7}$$

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

$$\left[\frac{\partial^2}{\partial z_m^2}\left(\frac{1}{n_m}\frac{dn_m}{dt}\right)\right]_{z_m=\hat{z}=z_c^*} < \left[\frac{\partial^2}{\partial \hat{z}^2}\left(\frac{1}{n_m}\frac{dn_m}{dt}\right)\right]_{z_m=\hat{z}=z_c^*}. \tag{C 8}$$

Appendix D

Beginning with equation (2.16), we look to find when interspecific competition speeds adaptation towards the optimal $z^* = z_n^*$. Dropping the arguments of the functions and denoting $\partial/d\hat{z}$ with prime, equation (2.16) reads

$$\frac{d\hat{z}}{dt} = \frac{-\mu\sigma_\mu^2}{2}[k-C]R\left[\frac{k'-C'}{k}\right] \tag{D 1}$$

and

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

Since in the one-population case $d\hat{z}/dt = (-\mu\sigma_\mu^2 R/2)k'$ (equation (2.6)), competition will speed evolution when

$$\left|\frac{(k-C)(k'-C')}{k}\right| > |k'|. \tag{D 3}$$

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

$$|k'-C'| > \frac{k}{k-C}|k'|, \tag{D 4}$$

yielding equation (2.17).

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