Evolutionary rescue in a consumer-resource system: Adaptation and persistence depend on the affected ecological traits

Abstract:

With evolutionary rescue, a population that is declining due to an environmental change subsequently adapts to its environment, avoiding extinction. Previous work has shown that negative density-dependence reduces the probability of evolutionary rescue. However, these models make several simplifying assumptions, either that selection acts strictly on intrinsic growth rates, r, or carrying capacity, K. Here, we simulate evolutionary rescue in a consumer-resource model, making explicit several ecological traits that may differentially affect r and K, and considering a self-replenishing resource. We demonstrate that the effect of density-dependence on rescue is indeed negative but weak, and declines with an increasing degree of maladaptation. The effect of density-dependence is also shown to be trait-dependent, since an environmental perturbation that reduces fitness may also increase or decrease resource competition. Furthermore, the relationship between Malthusian fitness following an environmental change and rescue probabilities depends strongly on the affected ecological trait, such that measurements of the rate of decline alone immediately following an environmental change are likely insufficient to predict rescue outcomes. Reductions in the conversion efficiency of resources into offspring are shown to be a greater hindrance to rescue than reductions in resource acquisition rates, whereas populations are able to tolerate substantial reductions in survivorship. Lastly, an abrupt environmental change that also impacts an evolving resource always hinders the evolutionary rescue of consumers, with reductions in resource

carrying capacity being more harmful than reductions in resource growth rates. This work improves our theoretical understanding of how ecology and evolution interact to affect evolutionary rescue.

Introduction:

Understanding the factors underlying the ability of populations to persist in response to environmental change is of utmost importance, particularly in light of the rapidly accelerating loss of biodiversity due to climate change (Berg et al. 2010, Bellard et al. 2012). One such mechanism of persistence is through evolutionary adaptation, or specifically evolutionary rescue (see Carlson et al. 2014; Bell 2017 for reviews), the process by which a population that is declining due to an environmental perturbation subsequently evolves and adapts to its new environment, avoiding extinction. Theoretical models of evolutionary rescue (hereafter ‘rescue’) are characterized by the concurrent modelling of both evolutionary and demographic processes, since successful rescue of a population is contingent on its rate of adaptation outpacing its rate of demographic decline (Gomulkiewicz & Holt 1995). For the most part, rescue models have considered a single isolated species evolving to avoid extinction (e.g. Gomulkiewicz & Holt

1995; Burger & Lynch 1995; Lande & Shannon 1996). These models have recovered many important insights into the factors underlying persistence, including the positive roles of additive genetic variance in fitness and of initial population size. Later work has extended this theory to consider in detail the effects of population structure (Uecker et al. 2014), recombination (Uecker & Hermisson 2016), selfing (Uecker 2017), and various other factors (Orr & Unckless 2008, 2014; Lachapelle & Bell 2012; Osmond et al. 2020; Xu 2023). The simplifying assumption of a single species existing in isolation, however, fails to capture ecological interactions among individuals such as predation and competition.

Ecological interactions among species may drastically influence demographic and evolutionary outcomes, and therefore rescue probabilities. For example, predation imposes a demographic cost on a prey species, accelerating its demographic decline if it is in need of rescue. However, predation may also positively influence prey rescue if predators preferentially consume maladapted individuals–accelerating the rate of prey adaptation–and the selective benefit outweighs the demographic cost (Osmond et al. 2017). A similar concept also applies if maladapted individuals experience greater interspecific competition (Osmond and de Mazancourt 2013). Moreover, complex dynamics may arise in co-evolving competitors. For example, a species with a smaller population size may have a higher chance of rescue than a competitor with a larger population size if the resource distribution evolves towards its optimum and away from its competitor (Van Den Elzen et al. 2017). This result is in apparent contradiction with the classic theoretical result of a positive relationship between population size and rescue (Gomulkiewicz & Holt 1995), thus underscoring the importance of considering a system's ecology.

Ecological interactions among conspecifics, particularly in the form of negative density-dependent growth, also likely reduce rescue probabilities (Chevin & Lande 2010, Osmond & de Mazancourt 2013, Nordstrom et al. 2023 Draghi et al. 2024). However, the magnitude of this effect remains controversial in the literature (Bell 2017). Simply defined, negative density-

dependence (hereafter ‘density-dependence’ for brevity) refers to the phenomenon where population growth declines with density, and may arise due to resource limitation, predation, pathogens, and various other factors. It was first argued by Gomulkiewicz & Holt (1995) that density-dependence would hinder rescue, since a population experiencing density-dependence would experience greater demographic decline than a density-independent population of equivalent size and fitness. However, a declining population may also experience ecological release due to relaxed density-dependence (Carlson 2014). For example, a rapidly declining population may experience a compensatory increase in the abundance of its biotic resource, potentially lessening or negating the negative effects of density-dependence on growth (Abrams 2002). Thus, it is possible that the effect of density-dependence is dependent on the rate of demographic decline and underlying mechanism of density-dependence. The effect of density-dependence due to competition for a self-replenishing resource on evolutionary rescue, however, remains unexplored in the rescue literature.

It is also worth noting that controversy over density-dependence may be explained in part due to differing model specifications (first described by Osmond & de Mazancourt 2013). Much of the theoretical work arguing a substantial effect of density-dependence on rescue has modelled selection as acting on intrinsic growth rates, r, modelling a logarithmic decline of density-dependent effects with population size (Chevin & Lande 2010, Nordstrom et al. 2023). Conversely, Boulding & Hay (2001) explored rescue outcomes using a model where negative density-dependence arises through linearly declining fecundity as a function of population size, instead concluding that negative density-dependence makes a small difference to rescue outcomes. Thus, we lack a clear theoretical expectation for the effect of density-dependence on rescue, and it will likely depend on specific features of the empirical system being studied.

While the above models may differ in certain mathematical specifications, all of them share a number of simplifying assumptions that obscure the relationship between demography and evolution. It is often either assumed that selection acts solely on intrinsic growth rates, r,

(Chevin & Lande 2010; Nordstrom et al. 2023) or population carrying capacity, K (Osmond & de Mazancourt 2013). However, these two parameters are likely not independent in reality (Pianka 1970, Mallet 2012, Travis et al. 2023), and there is much empirical evidence to suggest that r and K may co-vary positively or negatively due to varying life-history strategies in yeast (Wei & Zhang 2019), bacteria (Reding-Roman et al. 2017; Marshall et al. 2023), and spider mites (Bisschop et al. 2021). For example, selection acting to increase individual resource acquisition rates may increase r, but decrease K by reducing total resource availability among conspecifics at high densities (Agrawal & Whitlock 2012), thus intensifying density-dependence. However, selection acting to increase the efficiency of resource use would lead to a greater r as well as K by lowering the per-capita resource requirement for maintenance (Travis et al. 2023). In contrast, r-selected models of rescue assume that the intensity of negative density-dependence is solely a function of population size/density, and itself doesn't evolve (since K is held constant), thus neglecting the above relationships. Currently, we lack a theoretical framework to understand evolutionary rescue on ecological traits that may differentially affect r and K despite its widespread empirical evidence. This represents a major gap in our understanding of the effects of density-dependence on evolutionary rescue.

The use of mechanistic consumer-resource models represent a promising alternative framework to investigate the effects of density-dependence on rescue probabilities. Briefly, consumer-resource models explicitly track both consumer and resource population dynamics (see Sakarchi & Germain 2024 for a review). Consumer growth is a function of resource acquisition rates, the efficiency of their conversion into offspring, resource abundance, and mortality rates, whereas resource growth is often modelled using logistic growth minus their consumption by consumers. Selection can thus act on a consumer's resource acquisition rates, conversion efficiencies, or mortality rates, each with differing effects of the consumer's intrinsic growth rate and carrying capacity (Travis et al. 2023). While consumer-resource models

typically lack analytical tractability due to the explicit modelling of both consumer and resource dynamics as well as evolution, they facilitate a more mechanistic treatment of the effects of density-dependence on rescue. Moreover, we are able to investigate the effects of an environmental perturbation that also negatively impacts the growth of a focal species' resource, which to our knowledge remains unexplored in the literature.

In this paper, we investigate the effects of density-dependence on evolutionary rescue in a consumer following an abrupt environmental perturbation. Using a simulation-based approach, we investigate how density-dependence in the form of resource competition affects rescue in a consumer population experiencing viability or fecundity selection, the effects of an environmental change that also impacts a co-evolving resource, and the dependence of rescue outcomes on which life history traits are impacted in the consumer and resource. We find that density-dependence tends to weakly reduce rescue probabilities, generally agreeing with previous work on the topic. However, the relative effect of density-dependence declines as the magnitude of the environmental perturbation increases. We also show that the relationship between the rate of population decline following an environmental change and rescue probability depends substantially on the affected ecological consumer trait, with reductions in conversion efficiencies being most difficult to rescue from. Conversely, we find that populations are best able to rescue from decreases in survivorship, an effect previously observed by Draghi et al. (2024). Increases in mortality also generate a negative relationship between mortality and fecundity, a form of demographic compensation (Villelas et al. 2015), which has also been observed in species at range edges (Sheth & Angert 2018). Lastly, we show that an environmental perturbation that also negatively impacts resource growth always lessens consumer rescue probabilities, with decreases in resource carrying capacity generally being more costly to consumer rescue.

Methods

Model

Table 1. The definition of terms

Term	Meaning
N_t, R_t	Consumer and resource abundance at time-step t
λ_t	Consumer growth rate, or absolute fitness, at time-step t
λ_*	Consumer growth rate immediately following an environmental change
a	Consumer resource acquisition rate
C	Consumer resource conversion efficiency
S	Consumer survivorship
r_N	Consumer intrinsic growth rate
K_N	Consumer carrying capacity
r_R	Resource intrinsic growth rate
K_R	Resource carrying capacity
ϕ	Refers to any ecological trait (a, C, S, r_R, or K_R)
z_ϕ	Phenotypic trait value determining ecological trait ϕ
θ_ϕ	Optimum trait value for phenotype z_ϕ
$\theta_{\phi*}$	Optimum trait value for phenotype z_ϕ following an abrupt environmental change
ω^2	Measure of the width of Gaussian performance function
μ	Base-pair mutation rate
α^2	Variance in the effect size of a single mutation
V_M	Mutational variance: The total amount of new phenotypic variation introduced by mutation in a time-step
V_E	Environmental variance influencing each phenotypic trait

Ecology

We modelled the ecological dynamics of the system using a discrete-time consumer-resource model (MacArthur 1970; Abrams 2019). The use of discrete time instead of continuous time permitted the modelling of an explicit life cycle for forward-time, individual-based simulations. Assuming no evolution in the system for the time being, the ecological dynamics of the consumers are described by the following recurrence relation,

$$N_{t+1} = N_t(aCR_t + S), \quad (1)$$

where N_t is consumer abundance at time-step *t*, a is its resource acquisition rate, C is its conversion efficiency of acquired resources into offspring, R_t is resource abundance at time-step *t*, and S is survivorship/viability ($1 - m$, where m is the mortality rate). We model overlapping generations using a simple form of age-structure, with resource consumption followed by births and then deaths. Individuals are able to reproduce and are susceptible to mortality beginning the time-step following their birth, and individual fecundity, B, remains constant with age (note that $B = aCR_t$). An individual's growth rate, or absolute fitness, at time-step t, λ_t, is therefore $\lambda_t = aCR_t + S$, a function of an individual's fecundity, aCR_t, and its probability of survival, S. While fitness in a model of overlapping generations may be measured in many ways, including growth rates per generation or lifetime reproductive fitness, we focus on the population's Malthusian parameter, or $\ln[\lambda]$ (Fisher 1930; Kimura 1958). The Malthusian parameter most appropriately describes the rate of decline of the population per time-step, which is of most relevance to evolutionary rescue. The effects of changes in consumer ecological traits a, C, and S on consumer intrinsic growth rates, r_N, and carrying capacity, K_N, are described in Appendix A. The ecological dynamics of the resource are described by the following recurrence relation,

$$R_t = R_t(1 + r_R(1 - \frac{R_t}{K_R}) - aN_t), \quad (2)$$

where r_R is the intrinsic growth rate of the resource and K_R is its carrying capacity.

Briefly, our modelling of consumer dynamics differs slightly to the model described originally by MacArthur (1970, 1972), in that we do not explicitly consider a nutritive weight of the resource. We instead consider nutritive weight to implicitly influence the resource conversion efficiency, the exact value of which is unimportant given that we are only modelling a single resource type. Our model also considers mortality rates to be density-independent. This would be relevant in the case where most mortality is externally imposed, which we reason is likely the case in many scenarios that lead to rescue, but is indeed not necessarily the case.

Evolution

We model the evolution of these ecological traits of interest (a, C, or S in the consumer; r_R or K_R in the resource) using a discrete-time quantitative genetic model, commonly used in the evolutionary rescue literature (Gomulkiewicz & Holt 1995, Bürger & Lynch 1995, Boulding & Hay 2001, etc.). For most of our analyses, we only model the evolution of a single trait in the consumer, except in the case where we additionally model an evolving resource trait. While this methodology neglects potential correlations among traits (e.g. a negative correlation between a and C), it allows us to investigate how rescue is influenced by which trait is affected, all else being equal.

We model an arbitrary phenotypic trait underlying each ecological trait ϕ. Each individual has an arbitrary phenotypic trait of value z_ϕ, the sum of the genetic contribution of n additive loci with additive effects and a normally distributed environmental effect with mean 0 and variance 1

($V_E = 1$). The ecological trait value, ϕ_i, of an individual *i* with trait value $z_{\phi,i}$ is then described by a Gaussian performance function:

$$\phi_i(z_{\phi,i}) = \phi_{max} exp[-\frac{(z_{\phi,i}-\theta_\phi)^2}{2\omega^2}], \quad (3)$$

where θ_ϕ refers to the trait optimum corresponding to the maximal value of ϕ, and ω^2 is a measure of the width of the function, which was held constant among all traits. Mutations are drawn from a Poisson distribution at per-locus rate μ, with the effect size being drawn from a normal distribution with the mean corresponding to the previous allele's effect size and a specified variance of $0.5V_E$ (i.e. a Gaussian mutation scheme; see Johnson & Barton 2005). To simplify the model, the mutational variances and widths of the performance functions were held constant among all evolving ecological traits across simulations, and we assumed that the optimal phenotypic value underlying the ecological trait is 0 prior to the environmental change. We discuss specific parameter choices in the *Simulations* section below.

Simulations

General Features

We ran individual-based forward-time stochastic simulations using SLiM v4.01 (Haller & Messer 2022). Briefly, we initialized our simulations with the consumers and resources at demographic equilibrium. We then allowed our simulations to run for a period of 2,500 generations to reach mutation-selection balance for the ecological trait of choice, which varied depending on the experiment. In the next time-step, we introduced an abrupt change in environment by altering the initial optimal trait value, θ_ϕ, of one of the ecological traits ϕ (a, C, or S in the consumer; r_R or K_R in the resource), to $\theta_{\phi*}$, such that fitness following the environmental change was less than replacement, even at low density. To avoid extinction, the

population must reduce its genetic load by rapidly evolving toward its new optimal trait value, $\theta_{\phi*}$. Adaptation may have occurred via either standing genetic variation preceding the environmental change or de novo mutations following it. If the consumer population had not gone extinct by generation 10,000, we recorded the population as having been rescued.

The genomic architecture of each ecological trait in the consumers was modelled to be 100 genes split evenly among 10 chromosomes, with each chromosome of map length 30cM. Genes underlying a trait on a chromosome were evenly spaced and therefore 3cM apart. We modelled the genomic architecture of the resources to instead be composed of 10 freely recombining genes (i.e. an oligogenic trait). The relatively simple design of the resource genome was primarily chosen to minimize computational load, as resource abundance was on the order of 10^4.

We introduced demographic stochasticity in the simulations during the birth and death processes of consumers and resources and during the consumption of resources by consumers. The total number of births was Poisson distributed, with a mean of $N_t \underline{aC} R_t$ for the consumers and a mean of $R_t r_R (1 - \frac{R_t}{K_R})$ for the resources. Once the total number of offspring was established, parentage was retroactively assigned for the offspring using a multinomial distribution, with the probability of an individual being assigned parentage proportional to its fecundity. We modelled the death process in the consumers by drawing from a binomial distribution with the probability of survival equal to the individual's survivorship. We did not explicitly model resource death as its net growth is already captured by the r_R term, which we allocate to births for brevity. Resource consumption was modelled using a binomial distribution with $n = R_t$ trials and $p = aN_t$, the per-capita resource consumption rate.

Experimental Design

Effects of density-dependence on evolutionary rescue

We first investigated the effects of density-dependence on the probability of evolutionary rescue following an abrupt environmental change that negatively impacted consumer fitness (either through a decrease in a, C, or S). How is the effect of density-dependence on rescue influenced by the magnitude of environmental change and whether it is a, C, or S that are affected? We compared rescue probabilities between the consumer-resource model (Eq. 1 & 2; hereafter the *DD* model) and an equivalent model of density-independent growth (the *DI* model; Gomulkiewicz & Holt 1995), which we modelled by fixing resource abundance at its carrying capacity (i.e. $R_t = K_R$ for $0 \leq t \leq \infty$).

We must, however, limit consumer growth in the *DI* model such that it does not grow infinitely, which was done by enforcing a carrying capacity above which the density-independent population could no longer grow. Consumers in the *DI* model thus grew exponentially at a constant rate $r_N = aCK_R + S - 1$ until they reached their carrying capacity, K_N, above which their fecundity was reduced to 0 such that they were unable to grow beyond K_N (similar to the models of Gomulkiewicz & Holt 1995, Burger & Lynch 1995, and Orr & Unckless 2008). Consumers in the *DD* model, on the other hand, grew exponentially at rate r_N when at critically low density ($N_t \rightarrow 0$), but growth rates would linearly decline as they approached K_N (following Eqs 1 & 2). Both the *DI* and *DD* models were matched for K_N.

Effects of load on a, C, or S on evolutionary rescue

We investigated whether the relationship between mean fitness immediately following an environmental change and the probability of rescue were affected by which consumer ecological trait was impacted. We ran three sets of rescue simulations, varying the magnitude of the impact of the environmental change on one ecological trait while holding the others constant.

This approach allowed us to draw pairwise comparisons between simulations with reductions in fitness due to differing causes. In the first set, we modelled a to be negatively impacted by the environmental change and subsequently evolve, holding C and S constant. We did the same with C (holding a and S constant) and S (holding a and C constant). Ecological dynamics were governed by Eqs. 1 and 2 for all sets of simulations, and we also allowed for environmental effects to influence the phenotypes underlying the two non-evolving quantities (e.g. C and S in the first set).

The effects of load on an evolving resource on consumer evolutionary rescue

Lastly, we investigated the effects of an abrupt environmental change that also negatively influences the growth rates of a biotic resource, either by decreasing its intrinsic growth rates, r_R, or carrying capacity, K_R. We ran the simulations described above where we impose an abrupt environmental change that reduces consumer fitness (either through a reduction in a, C, or S), except that we also modelled a simultaneous decrease in resource intrinsic growth rates, r_R or carrying capacity, K_R. We modelled resource evolution similarly to consumer evolution. For each ecological trait in the resource (r_R or K_R), we modelled an underlying phenotypic trait whose value, z_ϕ, is the sum of the additive values of 10 loci and a normally distributed environmental effect with mean 0 and variance 1. The ecological trait value, ϕ_i, of a resource individual with trait value $z_{\phi,i}$ is described using Eq. 3.

In sum, we had three parameter sets overall: one without resource evolution, one where an evolving resource experiences a reduction in r_R, and one where an evolving resource experience a reduction in K_R. Within each parameter set, we varied which consumer ecological trait was affected ($a, C,$ or S).

Model Parameters

We modelled a slow growing consumer population, with a maximum consumer growth rate ($r_N = aCL + S - 1$) of $r_N = 0.03$ (Cortés 2016). The ecological parameters of our slow growing consumer population were: $a_{max} = 10^{-4}$, $C_{max} = 10^{-2}$, $S_{max} = 0.99$, $r_{R,max} = 0.5$, and $K_{R,max} = 10^5$. Individuals have high survival rates but low fecundity, characteristics that are commonly associated with K-selected species, for which we expect density-dependence to be most relevant. While our effect sizes may be sensitive this choice, the qualitative relationships between our variables, in terms of their effects on r_N and K_N, are not. The sole exception to this rule is the dependence of $\frac{dK_N}{da}$ on R_t ('resource over-consumption', see *Appendix A*), but we do not simulate this case. Consumer evolution was modelled using the following parameters: $\mu = 10^{-4}$, $\alpha^2 = 0.5$, $\omega^2 = 10$. Mutation rates and effect sizes were modelled to result in a relatively high mutational variance, V_m, according to empirical estimates (Johnson & Barton 2005); $V_m = 10^{-2}V_E$ here. Following an abrupt environmental change, rescue was therefore driven primarily by a few mutations of large effect, given that the variance in the effect size of a heterozygous mutation is $\alpha^2 = 0.5V_E$. Prior to the environmental change, however, these large effect mutations were highly deleterious and rapidly removed via selection, such that the amount of standing genetic variation was relatively low. In fact, much of the phenotypic variation for our traits prior to the environmental change was due to environmental variation (i.e. $V_P \approx V_E$).

For each replicate simulation, we recorded population sizes (N_t, R_t), mean consumer trait values ($\overline{a_t}$, $\overline{C_t}$, and $\overline{S_t}$), and mean resource trait values ($\overline{r_{R,t}}$ and $\overline{K_{R,t}}$) over time in a CSV file. Subsequent analyses of the recorded data and plotting were conducted in R 4.4.2. We compared the probability of rescue between the sets of the simulations for each change in optimal trait value by running a χ^2 contingency test for each pair of simulations.

Results:

The effects of density-dependence on evolutionary rescue

We ran simulations to compare rescue probabilities between a model of density-dependent and density-independent growth. Following an abrupt environmental perturbation that reduces consumer fitness, density-independent populations (hereafter *DI* populations) immediately experience maximal fecundity, whereas density-dependent populations (hereafter *DD* populations) must decline to critically low densities to experience maximal fecundity.

For the case where an abrupt environmental change negatively impacts consumer survivorship, S, we find the greatest absolute difference in rescue probabilities for a relatively weak environmental perturbation, $\theta_{S*} = 1.75V_E$ (Fig. 1). Despite both *DI* and *DD* populations exhibiting the canonical U-shaped trajectory of population size over time associated with evolutionary rescue, 69.7% [66.7, 72.4] of the *DI* populations experience rescue, compared to 56% [52.8, 58.9] in the DD populations. Indeed, we observe the relaxation of density-dependence as *DD* consumer populations decline, with density-dependent populations experiencing a steep rise in fecundity (Fig. 1C) due to increased resource availability (Fig. S1) following a decrease in fitness. However, there is still a lag to this release, as *DI* populations must first decline to a sufficiently low size, whereas *DI* populations are immediately able to benefit from maximal fecundity.

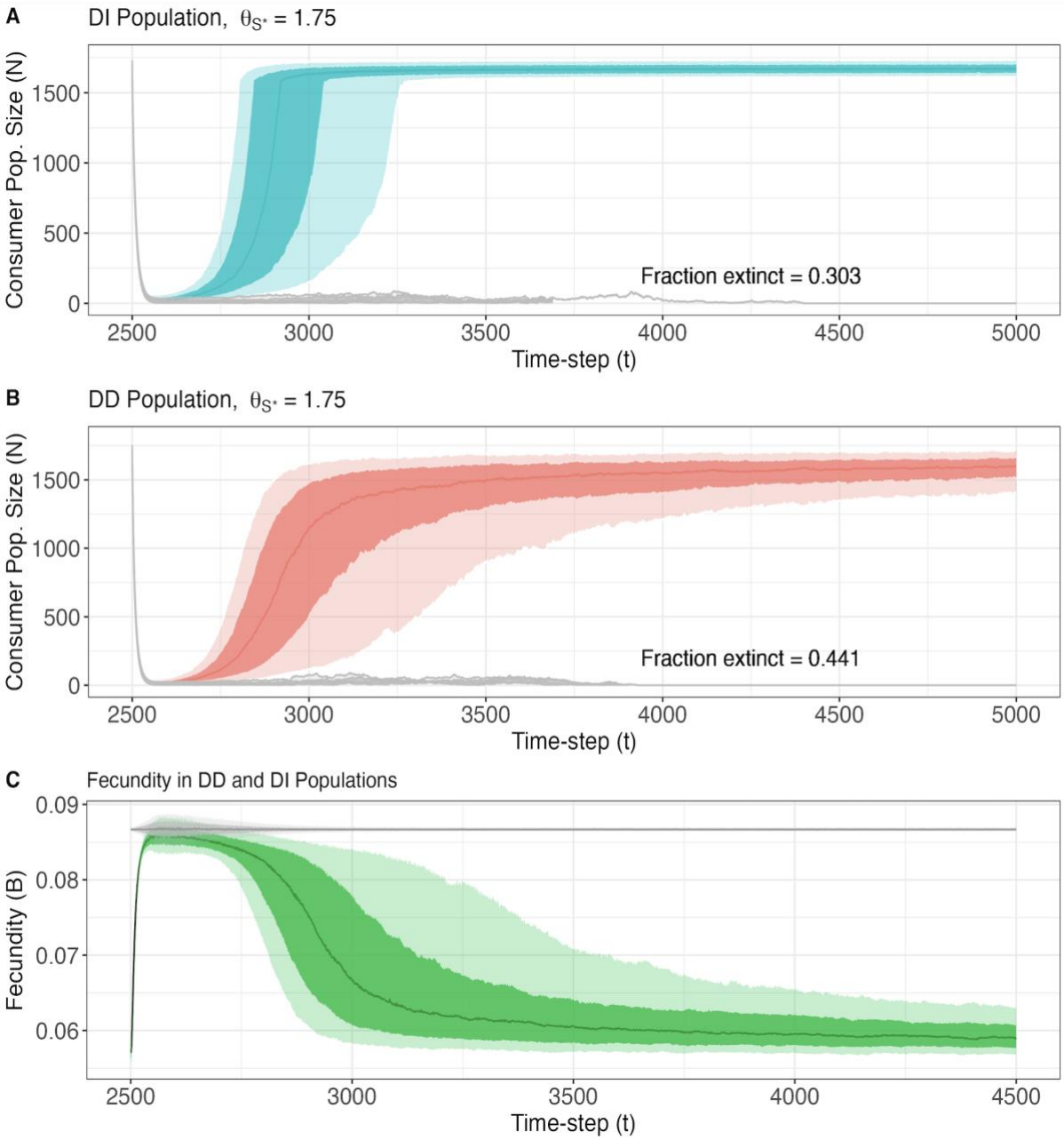

Figure 1. The effects of density-dependence on evolutionary rescue following a decrease in survivorship *S*. Consumer population size over time with $\theta_{S*} = 1.75V_E$ in (A) 1000 replicate *DI Model* simulations (blue) and (B) 1000 replicate *DD Model* simulations (red). The blue (red) line represents median population size, N_t, in the rescued *DI* (*DD*) populations across the 1000 replicates. The darker blue (red) shaded region represents the 25th and 75th percentile N_t, and the lighter blue (red) shaded region represents the 10th and 90th percentile N_t. The grey lines represent median N_t for the populations that went extinct. (C) Per-capita fecundity over time in the *DD* and *DI* simulations. The green (grey) line represents median fecundity, B, for *DD* (*DI*) populations. The darker green shaded region represents 25th and 75th percentile fecundity across the *DD* populations, and the lighter green shaded region represents the 10th and 90th percentile. (D) The fraction of replicates that were rescued in the *DI* versus *DD* simulations, with 95% confidence intervals calculated using the Agresti-Coull method.

Surviving *DD* populations also exhibit slower demographic recovery compared to *DI* populations (*cf.* Fig. 1A & 1B, see Fig. S2). As *DI* populations rescue, resource abundance declines, and density-dependent reductions in growth rate return. Thus, while rescue probabilities following an abrupt environmental change may be similar between *DI* and *DD* populations, *DI* populations recover faster. Additionally, as the magnitude of decline in survivorship increases, the absolute difference in probability of rescue between *DI* and *DD* populations declines (Fig. 2C), suggesting that the relative effect of density-dependence to reduce rescue probabilities decreases as the magnitude of environmental change increases.

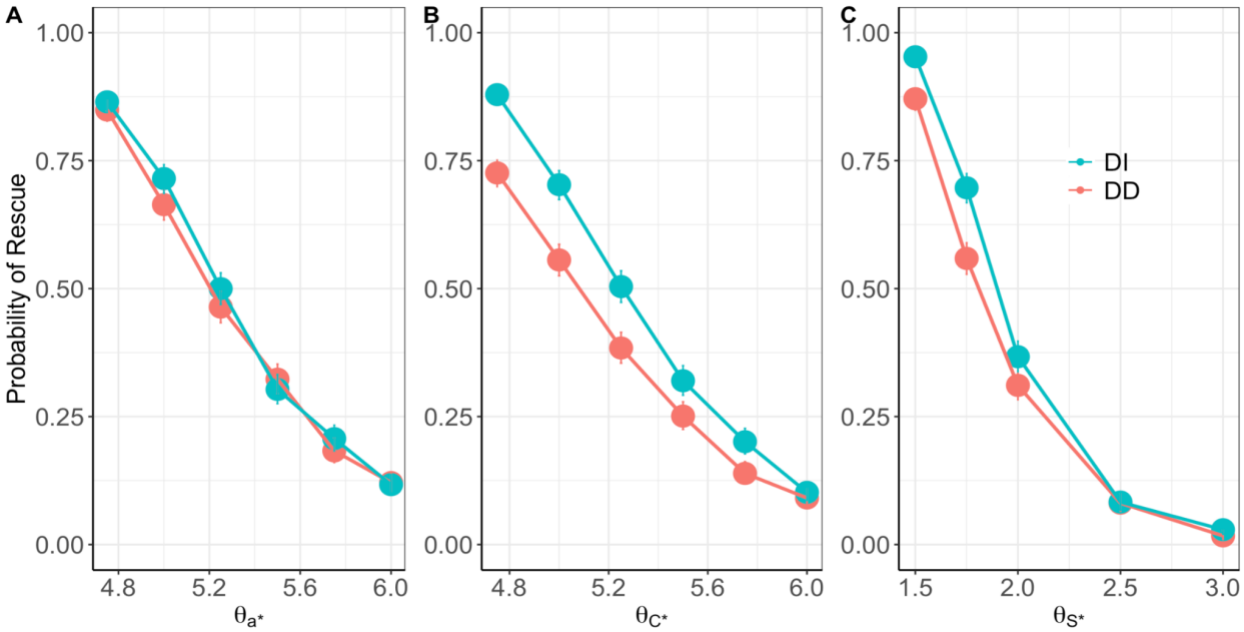

Figure 2. Rescue probabilities in *DD* versus *DI* populations. The fraction of simulated populations that successfully underwent evolutionary rescue following an abrupt decline in (A) resource acquisition rates, (B) resource conversion efficiency, and (C) survivorship. Rescue fractions for *DD* populations are in red, and rescue fractions for *DI* populations are in blue. 95% confidence intervals were estimated using the Agresti-Coull method. Abrupt environmental changes were imposed by shifting the optimal phenotypic value underlying the ecological trait θ. General model parameters can be found in the *Model Parameters* section of the *Methods*.

Reductions in resource acquisition rates, a, result in similar probabilities of rescue between *DI* and *DD* populations across all simulated magnitudes of environmental change (Fig. 2A), suggesting no discernible effect of density-dependence. In contrast, with a reduction in

resource conversion efficiencies, C, *DD* populations experienced lower rescue probabilities than *DI* populations for most magnitudes of environmental change, but they appear to converge as the strength of environmental change increases (Fig. 2B). Declining populations that experience a decrease in a benefit from maximum resource availability (i.e. $R_t = K_R$) at higher densities compared to populations that experience a decrease in C (Fig. S3), because, in the former case, resource growth benefits from both decreased consumer size (N_t) and per-capita consumption (a) (see the last term of Eq. 2). Thus, following a decrease in a, adapting populations experience ecological release sooner than populations experiencing a decrease in C, which is beneficial to evolutionary rescue. In *Appendix B*, we also show mathematically that a consumer population will always experience greater density-dependence due to a reduction in C versus a.

The effect of genetic load on a, C, or S on evolutionary rescue

Next, we explored how the probability of consumer rescue depends on whether the abrupt environmental change impacted resource acquisition rates a, resource conversion efficiencies C, or survivorship S in the *DD* model. Our simulations demonstrate that genetic load on C leads to a marginally lower probability of rescue than equivalent load on a (Fig. 3 inset), agreeing with our analysis in *Appendix B*. On the other hand, populations appear to be substantially more resilient to abrupt declines in S (Fig. 3 blue dots) than to reductions in a or C. For example, an immediate fitness decline of 0.33 due to a decrease in S results in similar rescue probabilities to an immediate decline in fitness of 0.04 due to a decrease in C (S: 0.081 [0.066, 0.010] vs. C: 0.091 [0.075, 0.110]). This suggests that the population growth rate immediately after the environmental change, λ_*, alone is an insufficient predictor of rescue probabilities. Instead, the relationship between a population's growth rate immediately following an environmental change, or, equivalently, its initial rate of decline, and rescue probability is

highly dependent on whether it is fecundity or mortality that are impacted, and to some extent how fecundity is impacted (Fig. 3).

We briefly explored to what extent the differences in observed rescue probability were a result of density-dependence acting on fecundity rather than mortality, an assumption of our model. We simulated mean time to extinction in the absence of evolution, complemented with numerical approximations (see *Appendix C*). We find that the median time to extinction does not appear to vary significantly among ecological traits (Fig. S4), suggesting that the differences in rescue between fecundity and mortality are primarily driven by differences in selection rather than density-dependence.

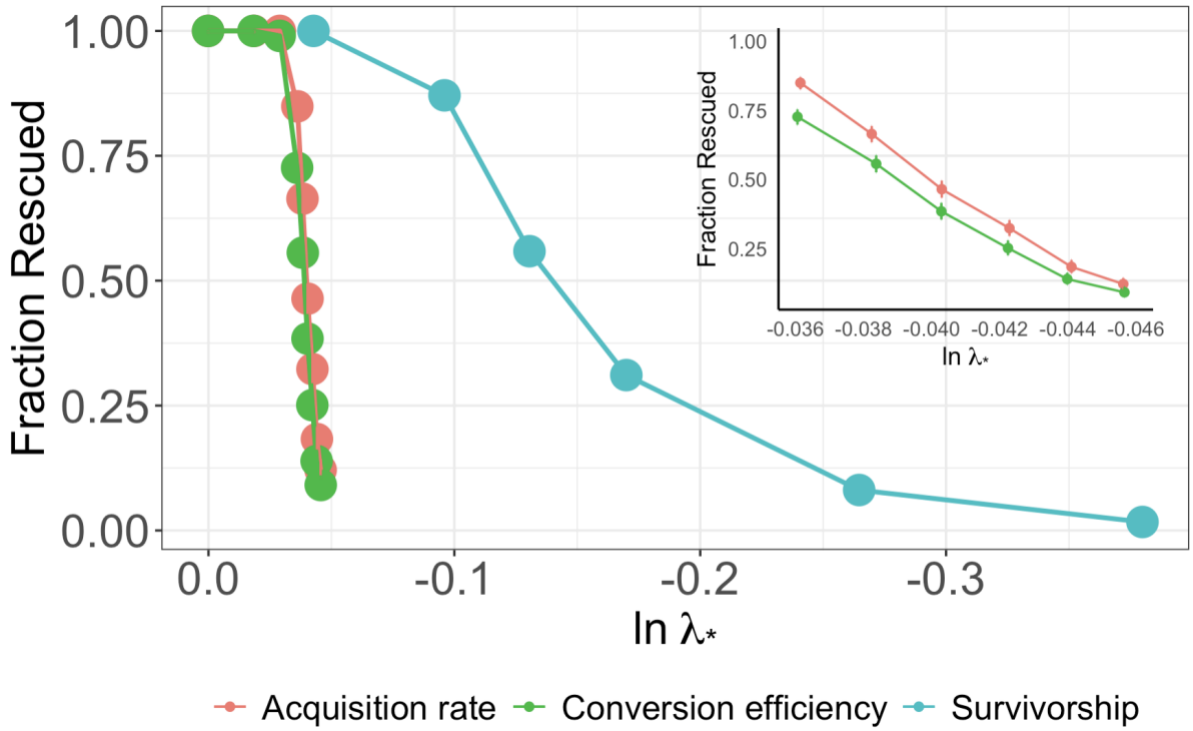

Figure 3. Rescue probabilities in *DD* populations as a function of the Malthusian parameter following an environmental change, $\ln(\lambda_*)$**.** The fraction of *DD* populations that were rescued following an abrupt environmental change that negatively impacted resource resource acquisition rates (red dots), resource conversion efficiency (green dots), or survivorship (blue dots), plotted as a function of mean fitness immediately following the environmental change, $\ln(\lambda_*)$. Each dot represents the fraction of simulated populations that were rescued from 1000 replicates, and bars represent 95% confidence intervals estimated using the Agresti-Coull method. For our resource acquisition rates and conversion efficiency simulations, we modelled $\theta_{a*} = \theta_{C*} = \{3, 4, 4.75, 5, 5.25, 5.5, 5.75, 6\}$, and for our survivorship simulations, we modelled $\theta_{S*} = \{1, 1.5, 1.75, 2, 2.5, 3\}$. General model parameters can be found in the *Model Parameters* section of the *Methods*.

We also observe a significant difference in rescue probabilities depending on whether the environmental change impacts resource acquisition rates or conversion efficiencies, which both underlie an individual's fecundity (Fig. 3 inset). Furthermore, as the average probability of rescue declines, populations experiencing a decline in acquisition rates have greater relative probabilities of rescue than populations experiencing a decline in conversion efficiencies. For the case where ln(λ_*) = -0.025, we observe that 84.9% [82.5, 87.0] of the acquisition rate simulations undergo rescue, whereas 72.6% [69.7, 75.2] of conversion efficiency simulations undergo rescue. This reflects an approximately 16.9% higher probability of rescue. For the case where $ln(\lambda_*)$ = -0.039, we instead observe a 32.9% higher probability of rescue in the acquisition rate simulations compared to the conversion efficiency simulations.

Since we simulate above a 'slow-growing' consumer population, we also investigated whether the differences in rescue probabilities between affected ecological traits translated to a 'fast-growing' consumer population (i.e. one with a higher r_N). To do so, we ran simulations with a different consumer parameter set, where $r_N = 0.18$. We found that the results were indeed qualitatively similar to the results presented in the main text, with load on survivorship and conversion efficiencies being the least and most costly to evolutionary rescue, respectively (Fig. S5).

The effects of genetic load on a co-evolving resource on consumer evolutionary rescue

Lastly, we explored the effects of an abrupt environmental change that also negatively impacts an evolving resource. We consider the simple case of a resource that experiences an abrupt decline in either its intrinsic growth rates, r_R, or carrying capacity, K_R, simultaneously with a consumer that experiences an abrupt decline in either its acquisition rates, a, conversion efficiencies, C, or survivorship, S.

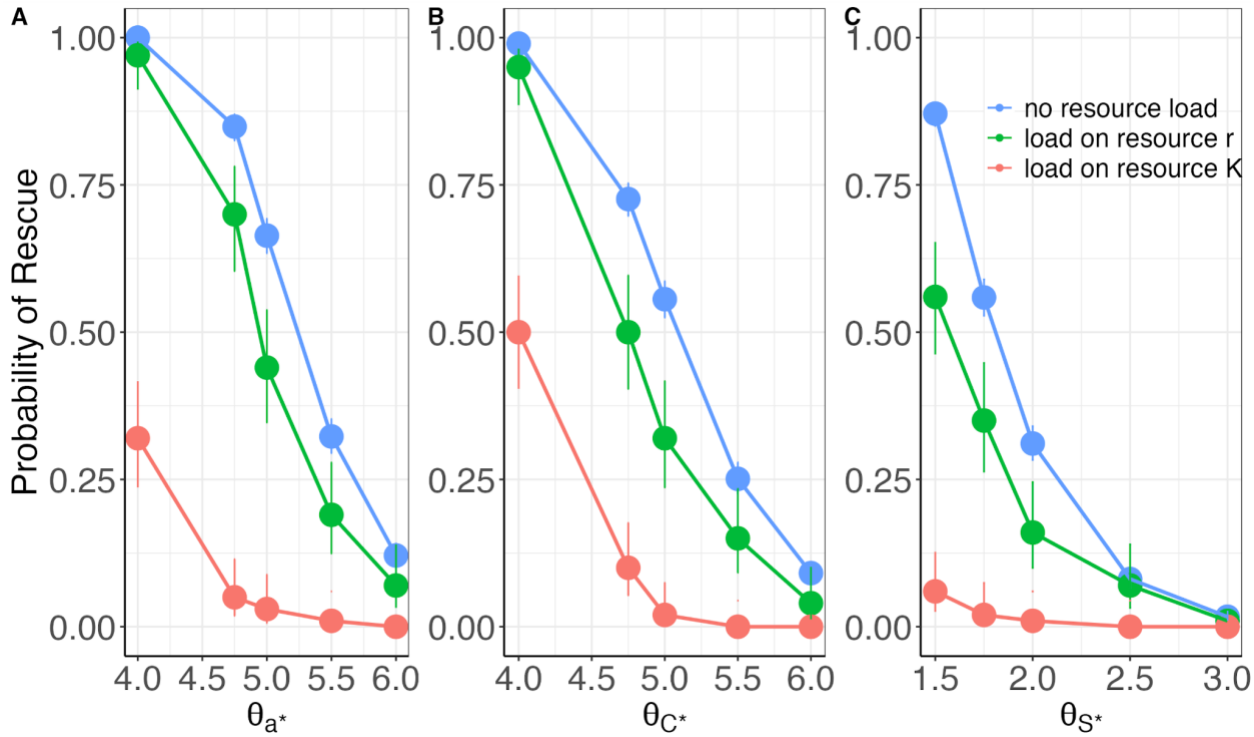

Figure 4. Probability of rescue when a co-evolving resource is affected. The probability of rescue for various magnitudes of environmental change when (A) a is affected, (B) C is affected, or (C) S is affected. The blue lines represent rescue probabilities when the resource itself is unaffected. The green lines represent rescue probabilities when the resource intrinsic growth rates, r_R, are also reduced ($\theta_{r_R^*} = 5$), and the red lines represent the case when resource carrying capacity, K_R, is reduced ($\theta_{K_R^*} = 2.58$). $\theta_{r_R^*}$ and $\theta_{K_R^*}$ were chosen such that mean fitness immediately following the environmental change, $\underline{\lambda}_*$, was equal among the two cases. General model parameters can be found in the *Model Parameters* section of the *Methods*.

We find that resource load decreases the probability of consumer rescue across all simulated parameters, with a reduction in K_R resulting in a lower probability of rescue in consumers than a reduction in r_R (Fig. 4). With a reduction in K_R, maximum resource abundance is reduced substantially, and consumers therefore experience lower fecundity even at low densities (Fig. S5). On the other hand, with a reduction in r_R, maximum resource abundance is unaffected, but is attained at a slower rate than when the resource itself is unaffected (Fig. S5).

Discussion

In this article, we show that the effect of density-dependence on evolutionary rescue is weak, but negative, in a consumer of a self-replenishing resource. We also make the previously unappreciated point that an environmental perturbation may itself reduce the intensity of density-dependence on a declining population. We have also shown that the relationship between the probability of consumer rescue and the population rate of decline varies strongly with the affected ecological trait, such that the rate of population decline immediately following an environmental change alone may be an insufficient predictor of extinction probabilities. In the case of density-independent mortality, we show that increases in mortality are most likely to lead to rescue. Conversely, declines in resource conversion efficiencies lead to the lowest chance of rescue, as individuals are unable to fully utilize increased resource availability. Lastly, an environmental change that also negatively impacts an evolving resource will always hinder consumer rescue.

Theoretical work on the effect of density-dependence on evolutionary rescue has mostly considered the evolutionary process as distinct from demographic processes (e.g. Boulding & Hay 2001; Chevin & Lande 2010; Nordstrom et al. 2023), representing a major simplification (which these authors are aware of). In reality, these processes are intertwined, and the outcome of rescue is likely to be dependent on the interaction between demography and evolution, given the substantial empirical evidence of varying relationships between r and K (e.g. Wei & Zhang 2019; Marshall et al. 2023). Moreover, the relationship between evolutionary adaptation and demography is highly dependent on the evolving ecological trait (Abrams 2019; Bisschop et al. 2022). In the context of rescue, the rate of population decline immediately following an environmental change is thus likely an insufficient estimator of future population growth and extinction, as this potentially neglects downstream ecological interactions experienced by the

population (Draghi et al. 2024), and ecological interactions between individual fitness and population growth.

We find an appreciable difference in the probability of rescue when resource acquisition rates are affected versus conversion efficiencies, two traits underlying fecundity. As populations suffer from decreases in resource conversion efficiencies, individuals must acquire more resources in order to maintain birth rates, thus intensifying density-dependence substantially. Conversely, as populations suffer from decreases in resource acquisition rates, they are able to experience more rapid ecological compensation. Interestingly, we also find a stark difference in rescue probabilities depending on whether it is fecundity or mortality affected. This has been observed before in the rescue literature by Draghi et al. (2024), who provide a convincing explanation. Briefly, an increase in mortality will accelerate the turnover of individuals in the population, hence reducing generation time and hastening adaptation. Conversely, a decrease in birth rates will reduce the turnover of individuals, lengthening generation time and slowing adaptation. More simply, individuals who experience lower fitness due to lower survivorship will be replaced by fitter individuals more rapidly than individuals who experience lower fitness due to lower fecundity. Given that we do not observe any meaningful difference in median times to extinction among ecological traits, it is likely that our observed differences are indeed a result of the differential rates of adaptation as described above.

However, it remains unclear in the first place what specific trait may be affected by an environmental change. There is some evidence to suggest that the dependence of evolutionary adaptation through a specific ecological trait varies with respect to its environment. Wei & Zhang (2019) show that quantitative trait loci (QTLs) in the yeast *S. cerevisiae* tend to show concordant effects on r and K (r/K trade-ups) in lower quality environments, but negative effects (r/K trade-offs) in higher-quality environments. They propose an explanatory model characterized by trade-offs between ATP production rates and utilization efficiency in the context of cell maintenance and division. Briefly, they propose a non-monotonic relationship

between intrinsic growth rates, r, and resource usage per cell per generation, which we define as ψ (they define this as C, which we have already used to denote conversion efficiency). Under low quality environments, r is low, and the evolution of increased r decreases ψ, thus increasing both r and K. This aligns with the predictions of our model, where an increase in conversion efficiencies, C, will increase both r and K. Conversely, in a high quality environment where r is already high, ψ increases with increasing r. Here, the population is instead dominated by competition for the acquisition of resources, which indeed aligns with the consumer-resource expectation that selection for resource acquisition rates, a, may result in r/K trade-offs.

While their model specifications may differ from ours in some ways, evolutionary rescue experiments in *S. cerevisiae* may be a possible avenue to test the predictions of our model. Empiricists could bias rescue towards potential life history strategies by controlling environmental quality. Declining yeast populations subject to an environmental stressor may perhaps be more likely to adapt through increases in resource conversion efficiency, C, in a low quality environment, or through resource acquisition rates, a, in a high quality environment.

Consumer-resource models offer useful mechanistic insight into the relationship between ecological traits and fitness, with ecological traits having the potential to affect both consumer intrinsic growth rates and carrying capacities differently. Despite this, our model has a number of limitations. To begin, we model a resource with the capacity to replenish itself, such that resource abundance is able to increase as consumer populations decline. While this is likely the case in many natural systems, as in the case of any herbivore and plant system, these results do not apply to the case of a consumer of a finite, non-replenishing resource, such as bacterial populations consuming medium. Moreover, the assumption of logistic resource growth is arbitrary, and we do not consider other forms used in the literature, such as a chemostat model (e.g. MacArthur 1972, Abrams 2019).

We make a number of additional simplifying assumptions. First, we assume that consumer mortality is density-independent, a common assumption in consumer-resource models (e.g. Abrams 2019). However, mortality itself may be an increasing function of consumer abundance. When consumer density is high, it is likely that consumers with relatively lower acquisition rates may be in worse condition, and are therefore more susceptible to mortality. Moreover, we assume that ecological traits are independent among consumers. Additionally, it is plausible that consumer ecological traits have similar underlying genetic and phenotypic structures, which we neglect. Instead, we assume that only a single trait in the consumer or resource is affected by the environmental change. This approach allows us to investigate, all else being equal, the effect of an ecological trait on rescue, but neglects the case where multiple co-varying traits may be concurrently affected. We also consider the simple case of intraspecific competition for a non-substitutable resource, without direct interference among competitors, as well as type 1 functional responses in the consumer. We also do not explore the effects of interspecific competition among species on the probability of rescue. The relaxation of these assumptions would be a fruitful avenue of future theoretical investigation.

We have here provided an improved theoretical framework to understand how evolutionary rescue is influenced by the complex interplay between evolution and demography. Given that evolutionary rescue is essentially a race between demographic decline and evolutionary adaptation, the use of mechanistic models that provide increased biological realism is an important step forward in our treatment of populations at risk of extinction (Urban 2024), an increasingly relevant problem given the rate of climate change (Berg 2010). The work presented here extends our understanding of the various ways through which environmental pressures may impose ecological costs on evolving species as well as species they interact with, and the resultant influence on species persistence.

Appendix A: Density-dependence in a consumer-resource model.

Here we summarize the relationship of consumer ecological traits a, C, and S to consumer density-dependence, following the methodology described by Travis et al. (2023). We can find the equilibrium values of both consumers, $\hat{N}$, and resources, $\hat{R}$, through algebraic manipulation of Eqs. 1 and 2: $\hat{N} = \frac{r_R(1-\frac{\hat{R}}{K_R})}{a}$ and $\hat{R} = \frac{1-S}{aC}$. It becomes clear that the equilibrium size of the consumer (i.e. its carrying capacity) is a function of the ratio of the per-capita rate of resource replenishment (numerator, $r_R(1-\frac{\hat{R}}{K_R})$) and per-capita rate of consumption (denominator, a), whereas the equilibrium size of the resource is dependent solely on the three potentially evolvable parameters of the consumer. Here density-dependence in the consumer arises via competition for a finite resource pool. As consumer population size grows the total consumption rate of resources increases, and fecundity declines linearly with resource abundance. Growth would instead be considered density-independent if resource abundance were constant with respect to consumer density, leading to exponential growth.

Density-dependence in a consumer-resource model is more complex than that of a logistic model, given that consumer intrinsic growth rates, r_N and carrying capacity, K_N (Travis et al. 2023) share several underlying ecological traits. It is still, however, possible to develop intuition for these relationships by re-writing consumer ecological traits in terms of the logistic growth parameters r_N and K_N. We can first solve for r_N by considering a consumer population that is at a critically low size ($N_t \approx 0$). In this regime, resource abundance is effectively at its own carrying capacity ($R_t \approx K_R$ when $N_t \approx 0$), and consumer growth is effectively exponential. Plugging this resource abundance into Eq. 1, we see that the consumer intrinsic growth rate, r_N, is $r_N = aCK_R + S - 1$. Consumer carrying capacity may be calculated by considering consumer equilibrium size, which through rearrangement of Eq. 2 is found to be $K_N = \frac{r_R(1-\frac{\hat{R}}{K_R})}{a}$. We assume

that resource growth occurs on a substantially shorter time-scale that consumer growth, such that resources reach demographic equilibrium immediately following an abrupt environmental perturbation (separation of time scales, $R_t = \hat{R}$ for $0 \leq t \leq \infty$). This assumption allows us to account for how equilibrium resource abundance may itself change following an environmental change that affects a consumer, given that resource abundance is a function of consumer trait values ($\hat{R} = \frac{1-S}{aC}$). . Plugging in $\hat{R} = \frac{1-S}{aC}$ into our formula for K_N, we find that $K_N = \frac{r_R(aCK_R+S-1)}{a^2CK_R} = \frac{r_R r_N}{a^2CK_R}$. It then becomes clear that both r_N and K_N share several underlying parameters and are functions of one another. The assumption of independence between r_N and K_N thus leads to an incomplete understanding of the effects of density-dependence on rescue from previous work.

We begin by exploring how intrinsic growth rates vary with a decrease in consumer ecological trait values, finding that $-\frac{\partial r_N}{\partial a} = -CK_R$, $-\frac{\partial r_N}{\partial C} = -aK_R$, and $-\frac{\partial r_N}{\partial S} = -1$. Intrinsic growth rates all decline linearly with respect to a decrease in a, C, or S. The magnitude of decline in a and C are dependent on both K_R and each other. This is because a decrease in resource acquisition would reduce consumer growth proportional to the rate at which individuals were able to convert resources into offspring in the first place. A decrease in conversion efficiencies, on the other hand, would reduce growth proportional to the total number of resources being acquired in the first place. Survivorship is independent of density here, and has a 1-to-1 relationship with r_N.

We now turn to exploring how consumer carrying capacity is influenced by a decline in consumer fitness, focusing on the dependence of this relationship on resource abundance. Considering the effects of a decrease in resource acquisition rates, a, on carrying capacity, K_N, we recover

$$-\frac{\partial K_N}{\partial a} = -\frac{s(2(1-S)-aCK_R)}{a^3CK_R}. \quad \text{(A1)}$$

Given that all variables are positive, the right hand side of Eq. A1 remains negative only when $2(1-S) > aCK_R$. Assuming a separation of time-scales and substituting in $\hat{R} = \frac{1-S}{aC}$, this inequality simplifies to $\hat{R} > \frac{K_R}{2}$. Thus, a decrease in acquisition rates will lead to a decrease in consumer carrying capacity, therefore intensifying density-dependence, only when the new resource equilibrium is above half of the resource's carrying capacity. Conversely, a decrease in acquisition rates may lead to an increase in resource carrying capacity when the new resource equilibrium is below half of the resource's carrying capacity.

Considering the effects of a decline in resource conversion efficiency, C, on carrying capacity, K_N,

$$-\frac{\partial K_N}{\partial C} = -\frac{s\hat{R}}{aCK_R}, \tag{A2}$$

which is negative for all parameter sets, and a linear function of $\hat{R}$. Thus, the decline in carrying capacity due to a decline in conversion efficiencies is linearly proportional to resource abundance. If resource abundance is already low, then a decline in conversion efficiencies will be less costly, as individuals are already acquiring a low number of resources.

Considering the effects of a decline in survivorship, S, on carrying capacity, K_R, we find that

$$-\frac{\partial K_N}{\partial S} = -\frac{s}{a^2CK_R} \tag{A3}$$

which is also negative for all simulations presented in the main text. However, the effects of a decline in survivorship on carrying capacity are independent of density, unlike the case of a decline in resource conversion efficiencies (*cf.* Eq. A3 & A4).

While the logic above provides a reasonable starting point to understanding density-dependence in a consumer-resource model, it remains unclear how these predictions translate to evolutionary rescue. Evolutionary rescue is a process characterized by non-equilibrium processes, in the form of fluctuating demography and rapid evolution due to maladaptation. For

example, despite a decline in resource acquisition rates leading to a decrease in both intrinsic growth rates, r_N, and consumer carrying capacity, K_N, when resource abundance is high, subsequent evolution would then increase both r_N and K_N, thus accelerating growth.

Appendix B. The effects on carrying capacity of a reduction in a versus C.

In *Appendix A*, we found that a decrease in conversion efficiency, C, always decreases consumer carrying capacity, K_N, therefore intensifying density-dependence. Here we explore when a decrease in resource C will intensify density-dependence to a greater degree than a decrease in a. We can approximate the effects of a decrease in a or C on K_N using a first-order Taylor expansion around their initial values:

$$K_{N,a*} = K_N + \frac{\partial K}{\partial a}(a_* - a) \tag{B1a}$$

and

$$K_{N,C*} = K_N + \frac{\partial K}{\partial C}(C_* - C), \tag{B1b}$$

where a and C refer to mean acquisition rates before an environmental change (we assume no individual variation here for brevity), a_* and C_* refer to mean acquisition rates and conversion efficiencies immediately following an environmental change, and $K_{N,a*}$ and $K_{N,C*}$ refer to consumer carrying capacities following a reduction in a or C, respectively. Thus, $K_{N,C*} < K_{N,a*}$ when

$$\frac{\partial K_N}{\partial C}(C_* - C) < \frac{\partial K_N}{\partial a}(a_* - a). \tag{B2}$$

In our simulations, we model a proportional reduction in both ecological traits a and C such that they are matched for mean fitness following the environmental change. Thus, $C_* - C = C_{max}(e^{-\frac{\theta^2}{2\omega^2}} - 1)$ and $a_* - a = a_{max}(e^{-\frac{\theta^2}{2\omega^2}} - 1)$. We can substitute the above values and simplify the inequality to

$$-\frac{\partial K_N}{\partial C} C_{max} < -\frac{\partial K_N}{\partial a} a_{max}. \quad \text{(B3)}$$

Next, we substitute in the right hand sides of Eqs. A1 and A2 and get the following inequality:

$$a_*(1-S)C_{max} > C_*[2(1-S) - a_* C_* K_R] a_{max} \quad \text{(B4)}$$

We can simplify with consideration that resource abundance following an environmental change, R_*, is $R_* = \frac{1-S}{aC}$ under the assumption of time-scale separation. Then we find that the above inequality is true when $R_* < K_R$, which is always true except in the case of an extinct consumer. Thus, a reduction in resource conversion efficiency will always entail a greater reduction in carrying capacity, K_N, than a proportional reduction in resource acquisition rates.

Appendix C. Time to extinction in the absence of evolution.

Here we briefly discuss how we calculated the time to extinction in a consumer-resource model, in the absence of evolution. In *Appendix A,* we use a simple heuristic argument to show that consumer growth can be re-written in logistic growth terms r_N and K_N, where $r_N = aCK_R - m$ (where $m = 1 - S$) and $K_N = \frac{r_R r_N}{a^2 C K_R}$. Given that the mean number of births and deaths per time-step is reasonably low in our model, we can approximate the population growth rate to be

occurring in continuous time, such that $\frac{dN}{dt} = r_N(1 - \frac{N}{K_N})$. Substituting in our values of r_N and K_N, and performing some algebraic manipulation, we find that $\frac{dN}{dt} = aCK_R(1 - \frac{aN}{r_R}) - m$, where $R = K_R(1 - \frac{aN}{r_R})$. This formula makes it clear that density-dependence in the system arises through limited resource availability influencing consumer fecundity, which represents a balance of resource consumption by consumers (aN) and replenishment by the resource (r_R). Returning to the continuous-time logistic growth model, it has a well-known general solution of the form $N_t = K_N \frac{N_0}{N_0 + e^{-r_N t}(K_N - N_0)}$. We can solve for the time to extinction, t_e, by plugging in $N_{t_e} = 0$, $r_N = aCK_R - m$, and $K_N = \frac{r_R r_N}{a^2 C K_R}$, which yields a deterministic prediction for the mean time to extinction in the absence of evolution. This method provides a reasonably accurate prediction, although it exhibits a slight upward bias (Fig. S4 triangles). This is to be expected since stochasticity will often reduce the time to extinction, as populations at low density that produce lower offspring than expected will achieve extinction much more quickly.

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Supplementary Figures:

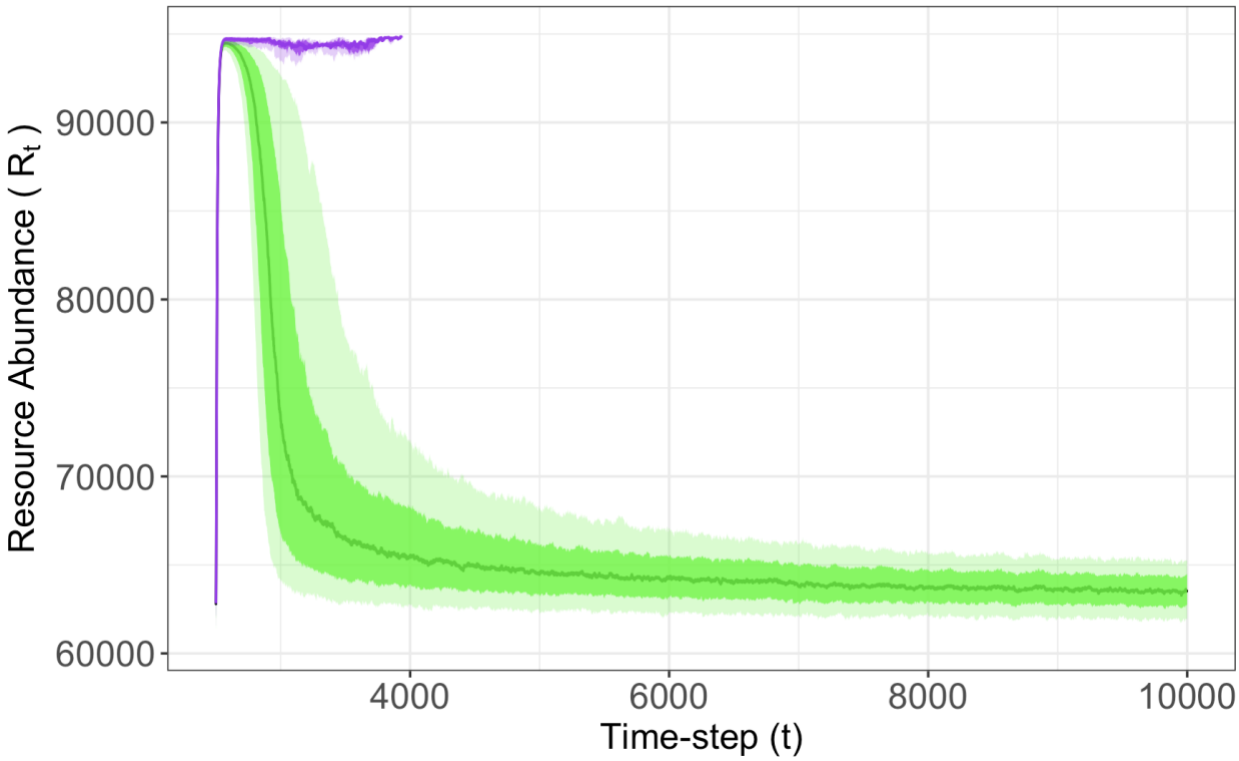

Figure S1. Resource abundance (R_t) over time (t) for the *Dynamic* simulations presented in Fig. 1 of the main text. The green lines represent replicates that survived, and the dark green line represents median population size, R_t, across the 100 replicates. The darker green shaded region represents the 25th and 75th percentile R_t, and the lighter green shaded region represents the 10th and 90th percentile R_t. The purple lines represent median R_t for the populations that went extinct.

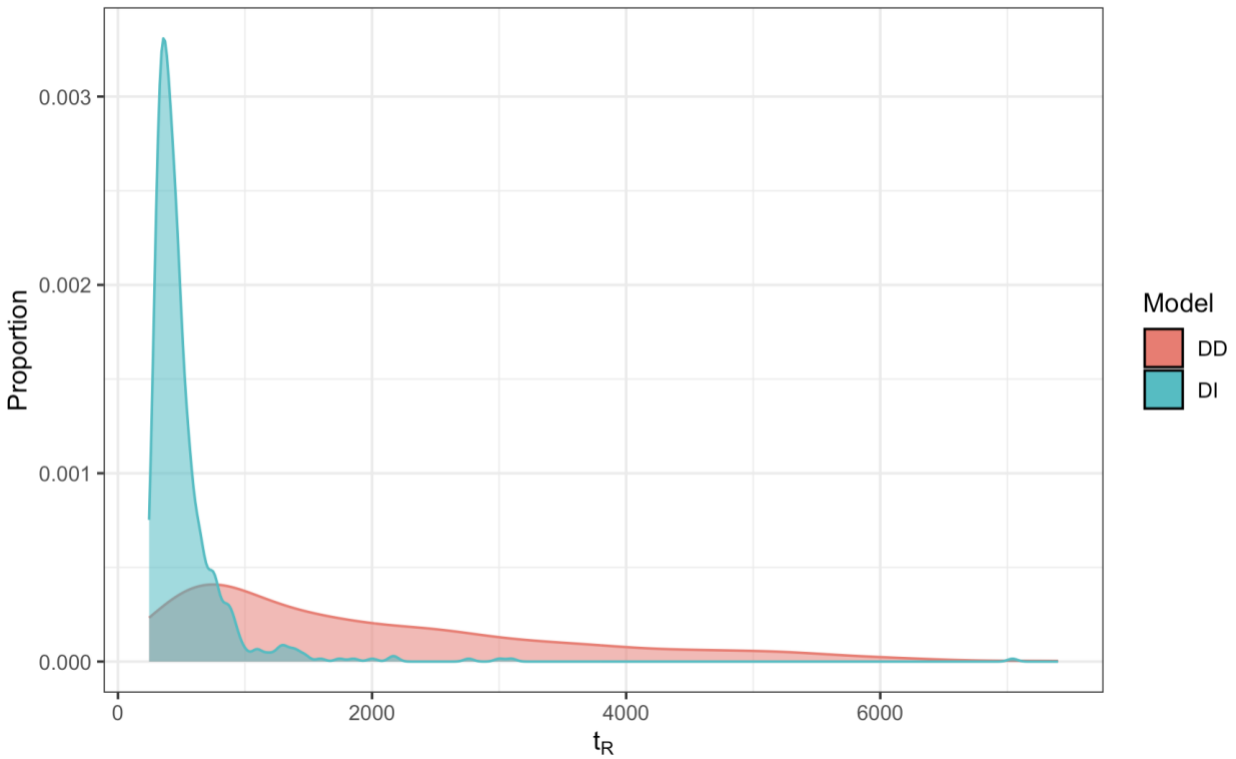

Figure S2. Time to recovery (t_R) in *DI* versus *DD* populations. The probability density functions for mean time to recovery (t_R), measured as the time it takes for a population to return to its prior population size following an environmental change that reduces fitness. The data used to make this plot was from 1000 replicate simulations with $\theta_{S*} = 1.75V_E$ in both the *DI* and *DD* populations, same as Fig. 1 in the main text.

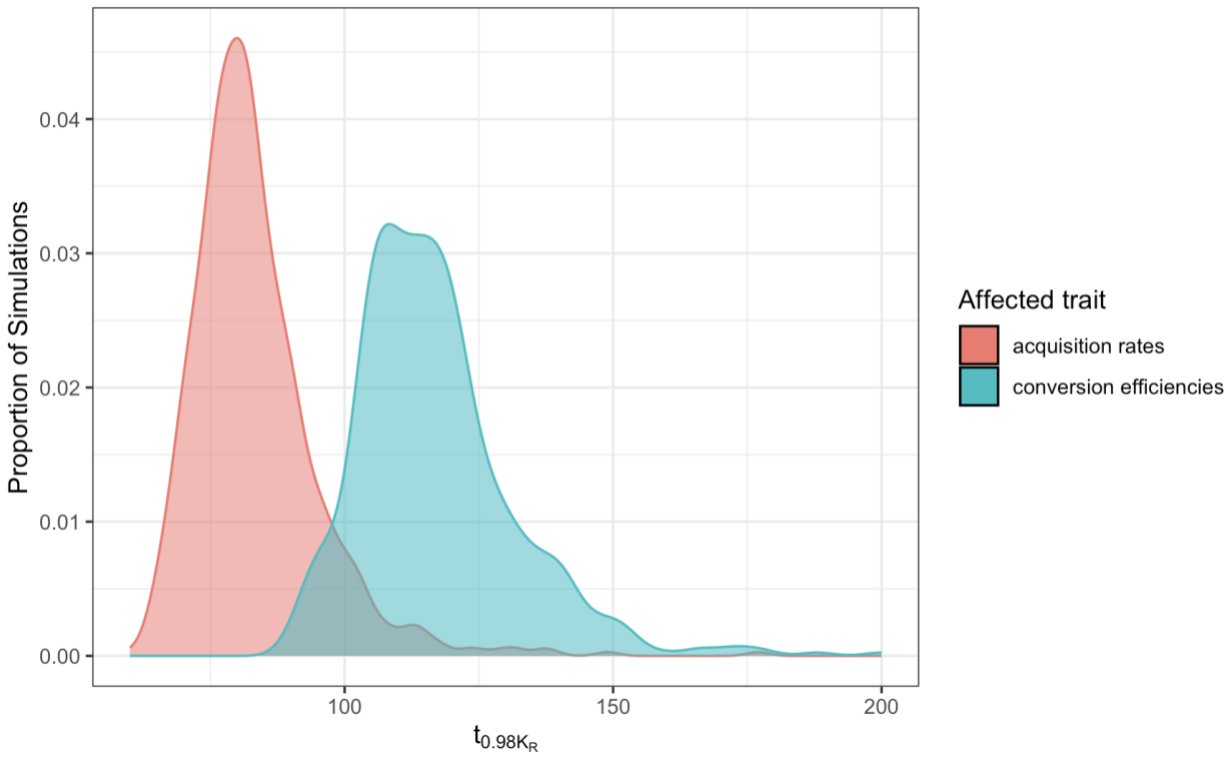

Figure S3. Time to max growth ($t_{0.98K_R}$) after an environmental change. The probability density function for the mean time it takes, following an abrupt environmental change, for resource abundance to be at least 98% of its carrying capacity (i.e. $R_t = 0.98\ K_R$). The red distribution describes the case where $\theta_{a*} = 5$, and the blue distribution describes the case where $\theta_{C*} = 5$.

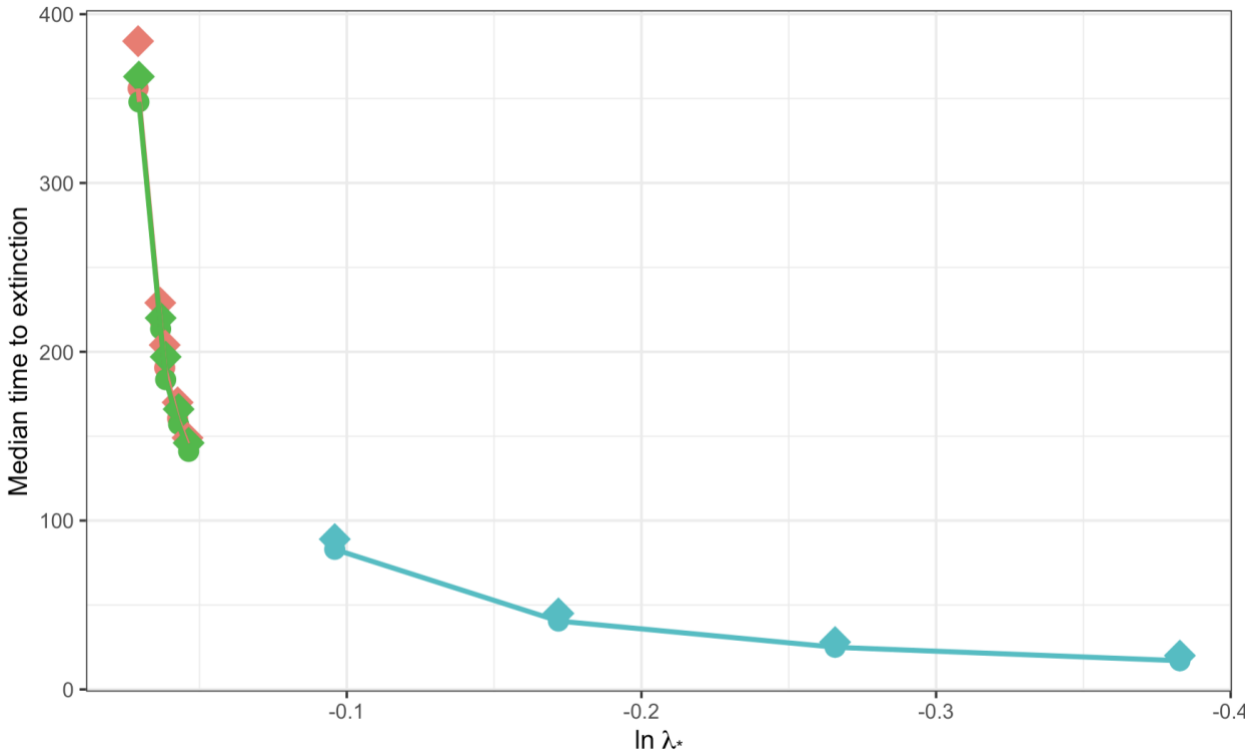

Figure S4. The median time to extinction, t_e, as a function of the Malthusian parameter immediately following the environmental change, $\ln(\lambda_*)$**.** Median time to extinction across 50 replicate simulations for simulations where resource acquisition rates are affected (red), resource conversion efficiencies are affected (green), and survivorship is affected (blue). The round dots connected by the lines represent values from the simulations, and the triangles represent numerical approximations under the assumption of time-scale separation between the consumer and resource.

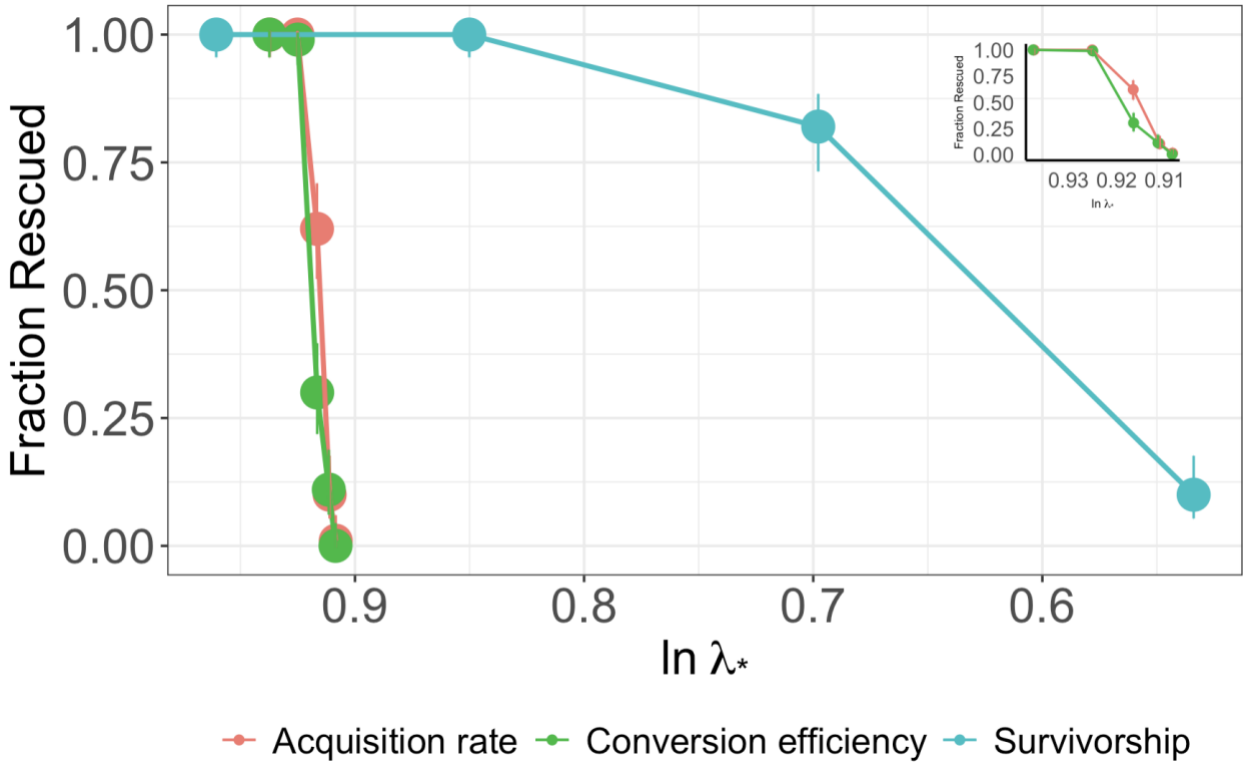

Figure S5. Rescue probabilities in *DD* populations as a function of the Malthusian parameter immediately following an environmental change, $\ln(\lambda_*)$**, for a consumer population with intrinsic growth rate** $\boldsymbol{r_N = 0.18}$**.** The fraction of *DD* populations that were rescued following an abrupt environmental change that negatively impacted resource resource acquisition rates (red dots), resource conversion efficiency (green dots), or survivorship (blue dots), plotted as a function of mean fitness immediately following the environmental change, $\underline{W_*}$. Each dot represents the fraction of simulated populations that were rescued from 100 replicates, and bars represent 95% confidence intervals estimated using the Agresti-Coull method. For our resource acquisition rates and conversion efficiency simulations, we modelled $\theta_{a*} = \theta_{C*} = \{5, 6, 7, 8, 9\}$, and for our survivorship simulations, we modelled $\theta_{S*} = \{1, 2, 3, 4\}$. The ecological parameters were as follows: $a_{max} = 10^{-4}$, $C_{max} = 10^{-2}$, $S_{max} = 0.9$, $r_{R,max} = 0.53$, and $K_{R,max} = 1.6 \times 10^5$, and the evolutionary parameters were identical to those found in the *Model Parameters* section.

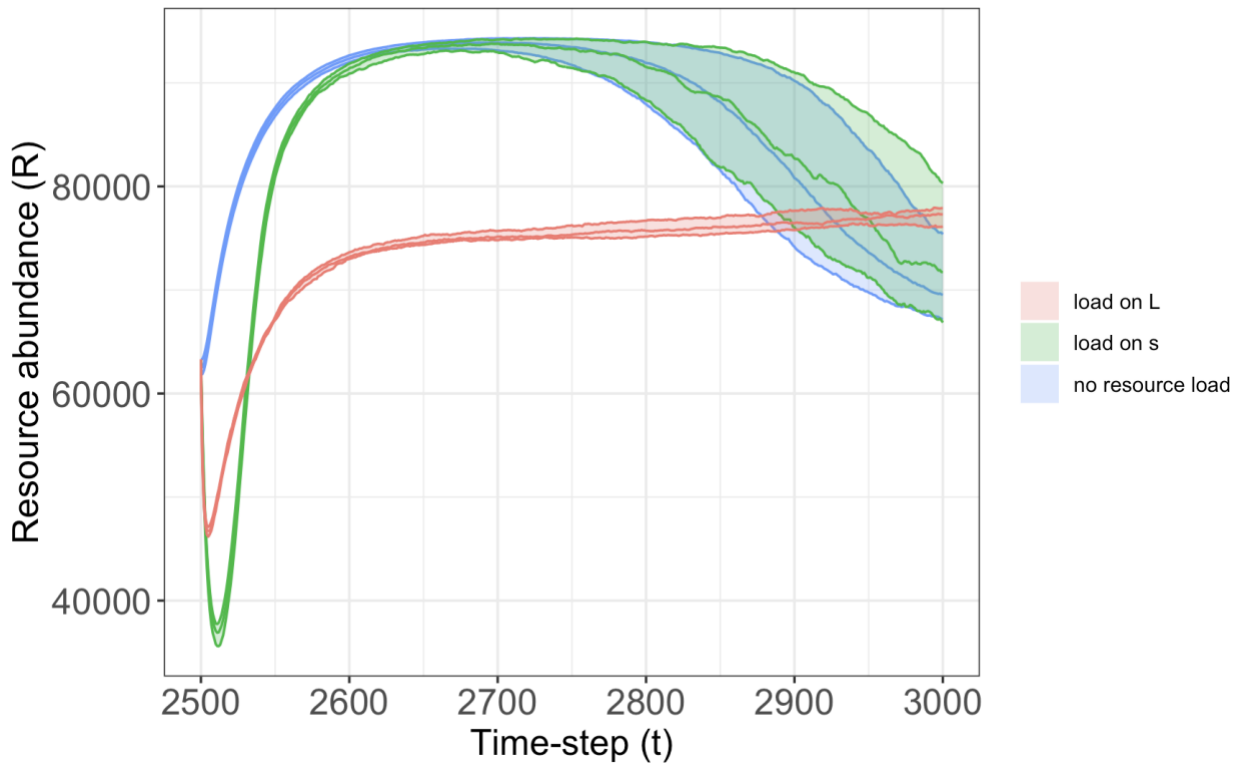

Figure S5. Resource abundance over time in an affected resource. Following an abrupt environmental change that reduces consumer resource conversion efficiencies, $\theta_{C*} = 4.75$, median resource abundance when the resource itself is unaffected ($\theta_{s*} = \theta_{L*} = 0$; blue line), resource intrinsic growth rates are affected ($\theta_{s*} = 5$; green line), and resource carrying capacity is affected ($\theta_{L*} = 2.58$; red line). The shaded regions represent that 25th and 75th percentile R_t