PNAS COMMENTARY

Evolution fails to rescue a population in an increasingly variable environment

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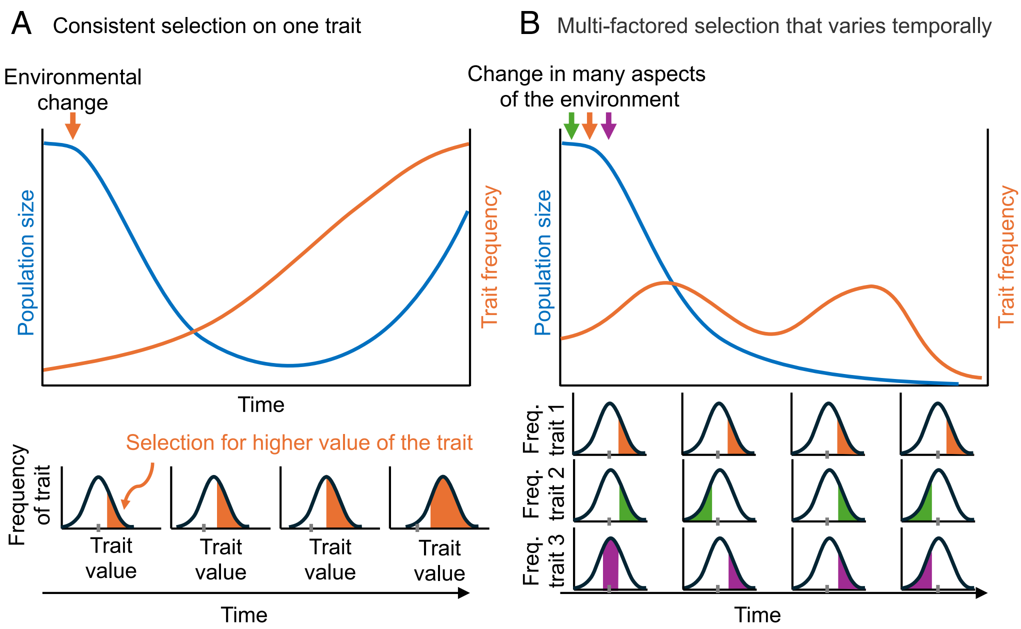

Fig. 1. (*A*) Evolutionary rescue following a single, consistent change in the environment and (*B*) no evolutionary rescue following changes in several aspects of the environment. The top graphs show population size through time and evolution of a trait important to fitness (or fitness itself) following environmental change. The smaller figures below illustrate the trait frequency distribution in the population at a given point in time, and the colored section indicates selection on individuals with different trait values. In (*A*), selection is consistent, leading to a shift in the trait frequency distribution toward higher trait values. In (*B*) different colors represent different traits that contribute to fitness and shifting selection pressures through time. This multifactorial selection on several traits varies temporally and includes trade-offs among traits such that even for traits where selection is consistent (in orange), no consistent increase in trait frequency (or fitness itself) occurs. The *Upper* portion of panel (*A*) is modified from figure 1 in ref. 4. Copyright (2014), with permission from Elsevier.

Environments around the globe have been fundamentally altered by human activities, affecting all species, even in remote areas. When environmental change is severe, the growth rate of a population can drop below the replacement rate, and the population will decline to eventual extinction unless the growth rate is able to increase again. Dispersal to higher quality habitat may be possible, but only if such habitat exists and the population is able to reach it. In the absence of dispersal, the only way populations can persist in the face of severe environmental change is by evolutionary adaptation to the altered environment. Such adaptation, which enables declining populations in altered environments to persist, is called evolutionary rescue (1). There is great interest in whether evolutionary rescue will help species survive global change, including habitat fragmentation, loss, and degradation (2–4). In PNAS, Clark-Wolf et al. (5) applied the theory of evolutionary rescue for the first time to a population of wild vertebrates, the charismatic Magellanic penguin, to evaluate whether adaptation to changing environments can rescue this population from extinction.

Evolutionary rescue leads to a characteristic U-shaped curve in populations size (Fig. 1). First, the population declines following environmental change, then adaptation leads to an increase in the frequency of beneficial traits, and a concomitant increased population growth, enabling population size to increase. Numerous theoretical and experimental studies show that rapid evolution can indeed prevent extinction following environmental change (e.g., 6 and 7), which provides hope for species of conservation concern. We know from these studies that the probability of rescue increases with genetic diversity and population size (e.g., 8) and decreases with negative density dependence (9) and a history of bottlenecks in population size (10).

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Author contributions: L.O. and R.A.H. wrote the paper.

The authors declare no competing interest.

See companion article, "Increasing environmental variability inhibits evolutionary rescue in a long-lived vertebrate," 10.1073/pnas.2406314121.

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Published September 3, 2024.

However, despite theoretical and experimental work suggesting that evolutionary rescue should be common, there are few examples from nature. The only likely examples fall into two broad categories: novel species interactions and strong anthropogenic selection. In the first category, a novel species is introduced (either purposefully or inadvertently) that gives rise to a new host–pathogen or host–enemy interaction. These species interactions, being novel, exert strong selection, and also entail potentially coevolutionary dynamics as both species can evolve. An example of this is rabbits and the myxoma virus (11). The virus was introduced deliberately to Australia to control overabundant introduced rabbits. Naive rabbit populations declined dramatically, but rather than going extinct, they rebounded following the evolution of resistance to the virus (12). The virus also evolved to become less virulent (13). Other such examples include rainbow trout and whirling disease (14) and field crickets and parasitoids (15).

Clark-Wolf et al. is the first study of evolutionary rescue in the wild to evaluate how natural abiotic shifts, including variability in these shifts, might affect the population and evolutionary trajectories of a long-lived animal.

In the second category, strong and consistent selection pressures are imposed by humans. The evolution of resistance in insects following pesticide treatment or use of transgenic crops that express toxins are examples of evolutionary rescue due to a strong and consistent selection (e.g., 16). Other similar cases include weeds and herbicides (17) and bacteria and antibiotics (18).

These examples thus always include strong and consistent selection, either biotic or abiotic, due to human activities. While climate change is leading to steadily warmer temperatures worldwide (and thus potentially fairly consistent selection), generally selection pressures experienced by natural populations vary over time and space (19) and are thus quite different from those that have been studied experimentally and theoretically to date. The variability of environmental change is little studied in research on evolutionary rescue and has only been incorporated in theoretical studies (e.g., 20 and 21). Yet, part of global change is an increase in extreme events and environmental variability. Furthermore, organisms with long generation times experience widely varying environmental conditions within a single life span. However, no study until now has tested the effect of environmental change on nonmodel organisms with long generation times, incorporating the variability of selection pressures over time.

Clark-Wolf et al. is the first study of evolutionary rescue in the wild to evaluate how natural abiotic shifts, including variability in these shifts, might affect the population and evolutionary trajectories of a long-lived animal. The authors use an impressive 38-year dataset following 53,959 Magellanic penguins (*Spheniscus magellanicus*) from southern Argentina. They combine remarkable data on survival, morphology (body size), demography, plume index (an oceanographic measure that drives selection on body size), and other aspects of the environment to estimate selection and evolutionary responses. Despite strong selection for larger body size imposed by long-term environmental change, under some conditions, smaller body size is favored, preventing morphological adaptation and evolutionary rescue. Projections of population size through time predict a decline to extinction without eventual adaptive evolution or human intervention. Interestingly, the authors demonstrate context-dependent and conflicting selection over time, where the same phenotypes are not always favored.

This study is particularly timely and interesting and makes several novel contributions. First, they evaluate the potential for evolutionary rescue in natural populations prior to population recovery. In contrast, the above examples of evolutionary rescue from natural populations were identified as such after the fact, rather than during population decline. But for the theory of evolutionary rescue to translate into predictions and guide management efforts, we need to understand the probability of rescue early following environmental change.

Second, Clark-Wolf et al. focus on a population experiencing uncontrolled environmental change in nature, rather than experimentally manipulated shifts in a lab or populations experiencing deliberately applied selection (e.g., pesticides) in nature as has been done previously. It is crucial to consider natural contexts as Clark-Wolf et al. do, given how widely selection pressure fluctuates over time (21). They find that selection on penguin body size changes with oceanographic conditions that sometimes favor larger and sometimes smaller body sizes. This likely makes evolutionary rescue impossible.

Third, they study a long-lived animal, where shifts in the environment occur within a single penguin's lifespan, such that no single penguin is likely to maximize its fitness, as the fitness optima shift through time. This is a crucial biological factor yet to be studied by theoreticians or experimentalists (12).

Finally, they include elegant and rigorous modeling of population fate using an IPM^2 model, which combines integrated population modeling with integral projection modeling. The authors use their model to assess whether evolutionary change in generation time or higher heritability in body size could facilitate rescue. They thus provide an outstanding example of how to combine data with models to obtain rigorous predictions essential for conservation.

Clark-Wolf et al. thus provide a roadmap for how to improve predictions of whether or not organisms will be able to adapt to our rapidly changing planet. Their work suggests an urgent need to move beyond asking, "What factors facilitate or constrain evolutionary rescue?" to asking, "Why is there a discrepancy between experimental and theoretical predictions and findings from nature?"

We suggest two key approaches used by Clark-Wolf et al. that will aid in understanding this discrepancy. First, it seems essential to describe the variability of environmental change experienced by natural populations, including reversible environmental change, autocorrelation, and extreme events, to be able to integrate it into research, including theoretical and experimental work in the laboratory. Second, study natural populations in context more often. This requires time and funding, but those are resources well spent indeed. Studies that include environmental and evolutionary processes are key to help safeguard the future of numerous species worldwide.

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