Review

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Evolutionary rescue in a changing world

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Evolutionary rescue occurs when adaptive evolutionary change restores positive growth to declining populations and prevents extinction. Here we outline the diagnostic features of evolutionary rescue and distinguish this phenomenon from demographic and genetic rescue. We then synthesize the rapidly accumulating theoretical and experimental studies of evolutionary rescue, highlighting the demographic, genetic, and extrinsic factors that affect the probability of rescue. By doing so, we clarify the factors to target through management and conservation. Additionally, we identify several putative cases of evolutionary rescue in nature, but conclude that compelling evidence remains elusive. We conclude with a horizon scan of where the field might develop, highlighting areas of potential application, and suggest areas where experimental evaluation will help to evaluate theoretical predictions.

A race against extinction

Under environmental change, population persistence hinges on phenotypic plasticity, dispersal, or adaptive evolution [1]. Although dispersal away from deteriorating environments [2] and immigration [3,4] might be sufficient to allow some populations to persist, dispersal limitations [5] and insufficient phenotypic plasticity indicate that adaptation will often be necessary to avoid extinction [6,7]. Adaptation that occurs quickly enough to prevent extinction due to maladaptation to a new environment is termed evolutionary rescue [8].

The overarching goal of this paper is to: (i) outline the diagnostic features of evolutionary rescue and distinguish it from other forms of rescue; (ii) synthesize the expanding knowledge surrounding evolutionary rescue revealed from theory (e.g., [8]) and experiments (e.g., [9,10]), highlighting the factors that influence the likelihood of rescue; (iii) provide likely examples of this phenomenon from natural and clinical settings that illustrate the dual nature of evolutionary rescue as both conservation ally and human welfare adversary; and (iv) highlight fruitful areas of further research and potential application.

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Hallmarks and brief history of evolutionary rescue

The diagnostic features of evolutionary rescue are a U-shaped demographic time series showing phases of decline, stabilization, and recovery and a corresponding increase in the frequency of an adaptive phenotype [8,11] (Figure 1). Evolutionary rescue might, however, occur without detection of the hallmark U-shaped curve because density-dependence or other environmental noise might mask its signal [9,12]. Conversely, following an abrupt environmental change, a population may exhibit a U-shaped population trajectory for ecological reasons; for example, because of time-lagged density dependence or because other species with negative interactions are likewise affected by the same environmental change. An essential ingredient in evolutionary rescue is that the rise in frequency of adaptive phenotypes/genotypes is causally responsible for the observed demographic rebound.

The historical roots of evolutionary rescue trace to Haldane [13] and Simpson [14], who mused on how quickly evolution might occur in nature. Half a century later, the contemporary mathematical framework of evolutionary rescue was initiated in [15], with the term 'evolutionary rescue' coined and theory formalized in 1995 in [8]. Evolutionary rescue is one of three commonly recognized forms of population rescue, which has led to confusion owing to

Glossary

Absolute fitness (population): the average number of surviving offspring produced per capita per time period (i.e., the λ growth parameter).
Adaptive evolution: transgenerational change in phenotype frequencies involving gene-frequency change due to selection on heritable variation.
Demographic rescue: increased probability of population persistence resulting from numerical addition of immigrants into a population sink.
Eco-evolutionary dynamics: the intersection of evolution, absolute and relative fitness, and ecological processes.
Environmental change: biotic and abiotic factors that alter the strength and form of selection.
Evolutionary rescue: genetic adaptation that allows population recovery from environmentally induced demographic effects that otherwise would have caused extinction.
Genetic rescue: increase in the absolute fitness of numerically small populations exhibiting inbreeding depression resulting from the influx of genetic variation from immigrants.
Migration load: an influx and accumulation of maladapted alleles from connected populations that retards population growth; synonymous with outbreeding depression.
Standing genetic variation: the number of alleles at a locus within a population.
Stochastic threshold: a heuristic 'rule of thumb' that describes a critical population size below which the probability of extinction due to environmental variability increases.

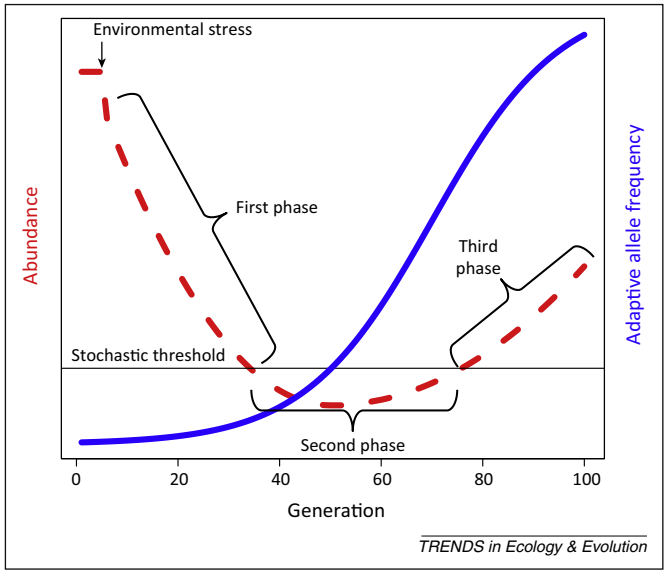

Figure 1. The hallmark features of evolutionary rescue: a U-shaped demographic trajectory with a corresponding increase of an adaptive allele frequency determining phenotypes that are robust to the new environment. In the first phase the population declines due to maladaptation to the new environment, in the second phase the population falls below the stochastic threshold below which it is increasingly susceptible to extinction owing from random fluctuations, and in the final phase positive growth is restored and the population emerges from below the threshold.

their apparent similarities. In Box 1, we outline the fundamental differences between demographic rescue, genetic rescue, and evolutionary rescue.

Synthesis of theoretical and laboratory research

Having clarified definitions in Box 1, we next review the rapidly expanding literature on evolutionary rescue and highlight the demographic, genetic, and extrinsic factors influencing the probability of evolutionary rescue revealed from theoretical and laboratory studies.

Lessons from theory

Demographic factors. Theoretical evaluations indicate that initial population size is a primary determinant of evolutionary rescue (Table 1) [8,16]. Population size governs the maximal rate of environmental change to which a population can successfully adapt [15,17] and influences the rate of evolutionary change in a population *per se* [17]. The heuristic concept of a stochastic threshold [8] describes a critical abundance level below which the probability of extinction increases due to stochastic processes. The more time a population spends below this threshold, the less likely evolutionary rescue is to occur [8], and the closer this threshold is to population carrying capacity, the longer the population will remain at risk of extinction [18]. The rate of population decline, influenced by the initial level of maladaptation, also affects the probability of evolutionary rescue: a rapidly declining population might drop below the stochastic threshold and tend toward extinction faster than the time required for an adaptive evolutionary response [19].

Density dependence and its interplay with dispersal can also influence the probability of evolutionary rescue. With positive density dependence [20], populations at low abundances are susceptible to Allee effects [21,22] that increase the risk of extinction due to demographic processes. Under this scenario, immigration to a sink population will increase population size and potentially alleviate Allee effects through, for example, an increased probability of mating, thereby increasing absolute fitness and the potential for evolutionary rescue [23]. By contrast, negative density dependence (e.g., logistic growth) is expected to lower equilibrial population size, thus increasing the potential for demographic stochasticity and functionally increasing the critical abundance below which persistence becomes increasingly unlikely [4]. However, it is important to note that negative density dependence may also buffer the reduction in fitness resulting from an environmental change, because the reduction in abundance should release the population from the density-dependent compensatory effects, leading to greater fitness relative to a population at equilibrium, thus counteracting the fitness reduction associated with the change. Importantly, [3] found that the inclusion of negative density-dependent effects substantially increased persistence time for simulated populations in the presence of dispersal. Generally, however, immigration into a sink population under negative density dependence is expected to increase intraspecific competition, dampen growth rate, and hinder adaptation.

Taken together, these studies indicate that the initial population size and level of maladaptation to the new environment both influence the probability of evolutionary rescue, as does density dependence and its interaction with dispersal, although these effects can increase or decrease the probability of evolutionary rescue depending on the context.

Genetic factors. A range of modeling exercises have revealed that standing genetic variation and genetic architecture, the rate of *de novo* mutation, and dispersal all influence the probability of evolutionary rescue. Greater standing genetic variation increases the probability of evolutionary rescue because it is immediately available for selection to act on [8,16,24]. However, standing genetic variation might lack the alleles that would permit persistence in a new environment and therefore be consistent with the assumption of a genetic constraint on evolutionary rescue (e.g., 'genostasis') [16,25]. By contrast, *de novo* mutation represents an alternative source of genetic variation but necessitates greater time to propagate. Greater mutation rate is predicted to be positively associated with the likelihood of evolutionary rescue, but only to the extent that mutation occurs at few adaptive loci and genetic diversity is limiting [26]. Indeed, the number of loci contributing to fitness and subsequently to evolutionary rescue is dependent on the underlying genetic architecture [27], although recent research highlights the structuring role of soft selective sweeps [28]. Finally, genetic correlations between fitness-related traits can accelerate or retard the rate of adaptation, but adaptation is faster, on average, when traits are positively correlated [29]. Conversely, genetic correlations were unexpectedly revealed to reduce the likelihood of evolutionary rescue in contexts that included dispersal [29].

Box 1. Distinguishing the forms of rescue

Considerable confusion surrounds the three forms of population 'rescue' common in today's literature. Here we distinguish among demographic, genetic, and evolutionary rescue and visualize the trajectories that lead to each form of rescue (Figure I).

Brown and Kodric-Brown popularized the term 'rescue effect' nearly 40 years ago to formalize the link between extinction probability and immigration [71]. This 'rescue effect' is now known as demographic rescue owing to the sole influence of dispersal leading to the numerical addition of individuals into population sinks, thereby preventing extinction. By itself, demographic rescue will not lead to recovery of declining populations, but it could lead to turnover. Immigration of dispersing individuals is also necessary for genetic rescue, but the contribution of immigrants in this context increases the viability of small populations that are suffering inbreeding depression as a result of novel genetic variation brought into the population [72]. Selective advantage of hybrids (heterosis) between local and immigrant individuals is the most commonly attributed mechanism of genetic rescue [56]. Genetic rescue is frequently revealed in cases where populations are at depressed levels due to genetic load due to inbreeding but are not necessarily experiencing negative population growth [73]. Because demographic rescue and genetic rescue are predicated on immigration, disentangling the two forms of rescue in nature is difficult and sometimes contentious [74,75]. By contrast, evolutionary rescue describes the scenario when adaptive evolution allows a population to recover from negative growth initiated by environmental change that otherwise would have caused extinction [76]. Thus, maladaptation following environmental change is central to evolutionary rescue. As a further distinction, evolutionary rescue necessarily results in the increased frequency of phenotypes that are robust to the new environmental conditions. Although evolutionary rescue was first examined in populations closed to dispersal [8], recent work has confirmed a role of dispersal in evolutionary rescue [9]. Immigration can facilitate evolutionary rescue by increasing standing genetic variation or, by increasing population size, immigration can increase mutational opportunities or alleviate positive density-dependent growth (i.e., Allee effects). By contrast, immigration during periods of negative density-dependent growth would reduce growth and hamper adaptation. The potential role of immigration in evolutionary rescue clarifies a fundamental misconception: genetic rescue and evolutionary rescue are not distinguishable based on the involvement of dispersal alone.

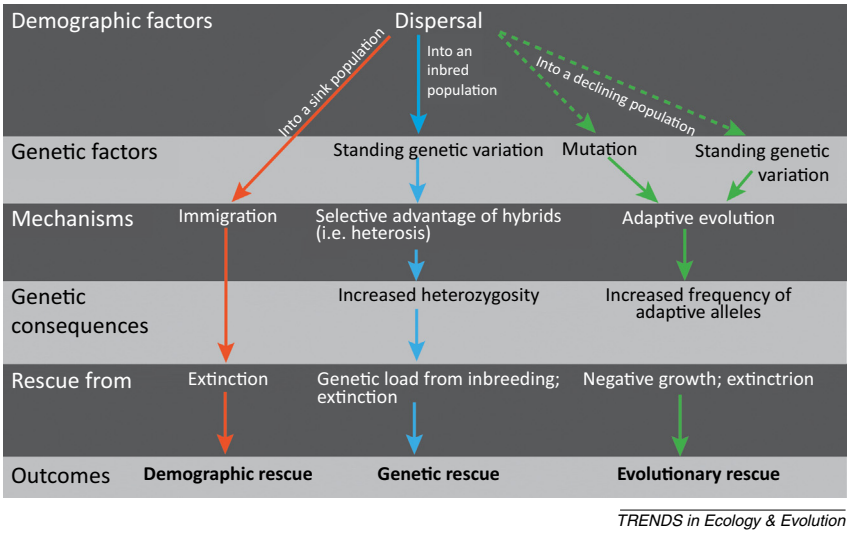

Figure I. Demographic and genetic factors, mechanisms, genetic consequences, and differences in what populations are being rescued from to distinguish among demographic rescue (orange pathway), genetic rescue (blue pathway), and evolutionary rescue (green pathway).

Theory predicts that dispersal between populations has the potential to enhance or reduce evolutionary rescue for genetic reasons. Generally, the effect of dispersal on the potential for evolutionary rescue is predicted to vary inversely with the ratio of the strength of selection to the rate of gene flow [30] and might depend on source–sink population dynamics [31]. More specifically, immigration is predicted to have a net positive effect on the probability of evolutionary rescue through the influx of novel genetic diversity [30] and by increasing mutational opportunities through increased population size [31]. Conversely, immigration is predicted to have a net negative impact in sexual reproducers due to migration load and resulting limitations on adaptive evolution from the influx of maladapted alleles in a heterogeneous environment [32–34]. Consistent with this, [35] found dispersal to be both advantageous, because it reduced competition experienced by adaptive mutant phenotypes dispersing into new environments, and disadvantageous if adaptive mutant phenotypes were emigrating out of the population. [36] also describes how emigration can limit adaptation in a sink population due to a reduction in abundance and the availability of beneficial alleles. Similarly, interspecies gene flow (i.e., introgressive hybridization) has the potential to increase or decrease evolutionary rescue depending on the fitness of hybrids, degree of assortative mating, and level of interspecific competition present [37].

The costs and benefits of dispersal in the context of evolutionary rescue are influenced by density dependence within populations. In the absence of negative density dependence, locally favored alleles will increase in prevalence (presumably facilitating evolutionary rescue) within the sink population if heterozygote fitness is greater than unity, independent of immigration rate and the fitness of other genotypes [4]. By contrast, in the presence of negative density dependence, the criterion for local adaptation is influenced by the rate of immigration and the fitness of other genotypes [4].

Extrinsic factors. The probability of successful evolutionary rescue is contingent on the rate of environmental change [16,38] relative to the generation time of the population [15]. The amount of standing genetic variation required for evolutionary rescue varies with the rate of environmental change and thus the selection pressure to which the population is exposed [16]. However, the influence of the rate of environmental change is context dependent, varying between scenarios of migration and the density-dependent fitness of migrants [35]. Moreover, the rate of environmental change links directly to the demographic factors considered previously; that is, when environmental change is rapid, the initial level of maladaptation will be large, leaving little time for adaptive evolution to restore positive growth [8].

Biotic interactions can also influence the probability of evolutionary rescue [39], with intraspecific competition (negative density dependence) expected to either: (i) hinder rescue due to the resultant decrease in abundance and thus mutational opportunity; or (ii) have no effect if the population is reduced to an abundance well below capacity following environmental change [18]. Conversely, interspecific competition can have a positive effect, resulting from stronger selection for successful alleles and thus an increased rate of adaptive evolution [18]. Beyond competition, predation is predicted to influence the probability of evolutionary rescue. Counter to *a priori* predictions, rescue was found by [40] to be more likely for both predator and prey populations across multiple rates of environmental change and selection strengths, probably due to the removal of maladapted individuals in both predator and prey populations.

Evolutionary rescue in the laboratory

Here we highlight the experimental tests of theoretical predictions regarding evolutionary rescue *in vivo*, which provide an important first step toward understanding the role of evolutionary rescue in nature.

Demographic factors. Laboratory experimentation with yeast (*Saccharomyces cerevisiae* [9,10] and *Saccharomyces paradoxus* [41]) and bacteria (*Pseudomonas fluorescens* [42]) have confirmed the theoretical prediction that populations exposed to an abrupt environmental change are more likely to recover when initial population size is large (Table 1). Also consistent with theoretical predictions, experiments have revealed that evolutionary rescue is most likely when the degree of initial maladaptation is small [10]. Three important factors remain untested: the amount of time a population can persist at low abundances before evolutionary rescue becomes improbable, generation time, and the role of density dependence in influencing the probability of evolutionary rescue (Table 1).

Genetic factors. Consistent with theory, laboratory studies have consistently confirmed that the amount of standing genetic variation is a critical factor influencing the likelihood of evolutionary rescue (Table 1). In the first experimental test of this prediction, rescue of wheat-adapted populations of a flour beetle (*Tribolium castaneum*) exposed to a novel corn flour resource was positively correlated with initial genetic variation [43]. Similarly, a unicellular green alga (*Chlamydomonas reinhardtii*) exposed to salt stress [44] and bacterial (*P. fluorescens*)

Table 1. Side-by-side comparison of theoretical and laboratory studies of evolutionary rescue, highlighting the demographic, genetic, and extrinsic factors that affect the probability of rescue[a]

	Theory/modeling results	Laboratory results
Demographic factors		
Initial population size	(+) [8], (+) [15], (+) [16]	(+) [9], (+) [10], (+) [41], (+) [42]
Time below stochastic threshold	(−) [8]	
Generation time	(−) [15]	
Negative density dependence	(+) [3], (–) [4]	
Positive density dependence with immigration	(+) [23]	
Genetic factors		
Standing genetic variation	(+) [8], (+) [12], (+) [24]	(+) [42], (+) [43], (+) [44]
Sexual reproduction		(+) [44]
Dispersal	(–) [30], (+/–) [31], (+/–) [35]	(+) [9], (+) [45]
Immigration	(–) [32], (–) [33], (–) [34]	
Emigration	(−) [36]	
Mutation rate	(–) [26]	
Genetic linkage	(–) [32]	
Initial maladaptation	(–) [8]	(–) [10]
Number of loci interacting to influence fitness (genetic architecture)	(+/–) [27]	
Extrinsic factors		
Rate of environmental change	(+) [77], (−) [16], (−) [38]	(−) [9], (−) [41], (−) [45], (−) [46], (−) [47]
History of environmental change		(+) [47]
Interspecific competition	(–) [18], (–) [39]	
Intraspecific competition	(+) [18]	
Predator–prey dynamics	(+) [18], (+) [40]	
Introgressive hybridization	(+/−) [37]	

[a]The (+) or (−) indicate whether the factor increases or decreases the probability of rescue, respectively.

populations exposed to antibiotics [42] were more likely to be rescued by adaptive evolution when standing genetic variation was high. Obligate sexual reproduction also increased the probability of evolutionary rescue in a green alga under experimental conditions [44]. However, further laboratory exploration of the influence of mutation rate and genetic architecture would be of great value in describing the genetic conditions under which evolutionary rescue might realistically be observed.

Despite theoretical expectation that dispersal can positively or negatively influence the likelihood of evolutionary rescue, laboratory evaluations with yeast [9] and a pathogenic bacterium (*Pseudomonas aeruginosa*) [45] both conclude that probability of rescue is increased with dispersal (Table 1). This contradictory result may have resulted through the use of clonal model organisms as maladapted clones are expected to go extinct and thus not likely to influence the probability of evolutionary rescue.

Finally, to date there have been no experimental demonstrations of the expectation that the 'migration load' arising from maladapted immigrants, suppressing adaptation by mating with better-adapted residents, has a sufficiently strong influence to prevent evolutionary rescue. Migration load almost certainly plays a critical role in determining the probability of evolutionary rescue, but experimental demonstrations are entirely absent.

Extrinsic factors. The rate of environmental change remains the extrinsic factor most thoroughly explored in experimental studies of evolutionary rescue, which unanimously conclude that evolutionary rescue is most likely under gradual environmental change [9,41,45–47] (Table 1). Lindsey *et al.* [46] explored the genetic underpinnings of this pattern by exposing replicate populations of *Escherichia coli* to variable rates of increase in antibiotic concentration. Not only were mutational trajectories distinct under variable rates of change, but certain genotypes were inaccessible under the most rapid environmental change because the path leading to each genotype depends on environmental conditions and is thus context specific. This result suggests that rapid environmental change might serve to eliminate the possibility that specific mutations necessary for persistence will arise at all.

The history of environmental change and exposure to past stress also influences the likelihood of evolutionary rescue, although this has only been studied in the experimental arena (Table 1). Adaptation to shifts in the environment is more likely when populations have a history of exposure to the stressor, such as yeast exposed to salt stress [47]. This finding is likely to stem from a reduced level of maladaptation in a population with prior exposure to the stressor, presumably a result of a greater genetic predisposition to recovery (i.e., favorable standing genetic variation). Beyond the rate and history of environmental change, the type of environmental change may also be important. As a recent example, [48] explored the consequences of pollinator loss for the predominately outcrossing *Mimulus guttatus*. Following pollinator loss, *Mimulus*,

Box 2. Rapid genetic adaptation without demography: did evolutionary rescue pass us by?

Rapid local adaptation in response to introduced predators represents a prime candidate system for detecting evolutionary rescue in wild populations, although often a lack of demographic data makes it unclear whether the demographic trajectory showed the expected phases of decline, stabilization, and recovery. In Figure I we highlight two putative candidates for evolutionary rescue where missing demographic time series preclude confirmation of rescue: threespine sticklebacks (*Gasterosteus aculeatus*) in Lake Washington, USA; and red-bellied black snakes (*Pseudechis porphyriacus*) in Australia. Following remediation of water quality and transparency in Lake Washington, the predatory efficiency of the visual hunting cutthroat trout (*Oncorhynchus clarkii*) increased and presumably exerted intense selection on their stickleback prey. Coincident with this change in the environment was a rapid shift toward more heavily armored anti-predator phenotypes in sticklebacks [78]. Sticklebacks are still abundant in Lake Washington [79], suggesting that evolutionary rescue might have facilitated their persistence in an increasingly risky environment. Rapid evolution of armoring is unlikely to be a panacea for rescuing all stickleback populations faced with novel predators, as evidenced by the extinction of a lightly armored population of stickleback following invasion by piscivorous northern pike (*Esox lucius*) [80]. On the other side of the globe, selection imposed by highly toxic cane toads (*Rhinella marina*) in Australia has apparently driven the genetic adaptation of increased resistance to toad venom by predatory red-bellied black snakes [81]. Cane toads were introduced to Australia in 1935 and quickly spread widely. Using a 'space-for-time' substitution design, [81,82] show adaptive shifts in heritable morphology, prey preference, and resistance among snake populations with longer periods of exposure to toads compared with naïve populations. Figure IA adapted, with permission, from [78]; Figure IB adapted, with permission, from [81]. Photograph credits: J. Kitano (sticklebacks) and J. Armstrong (cane toad).

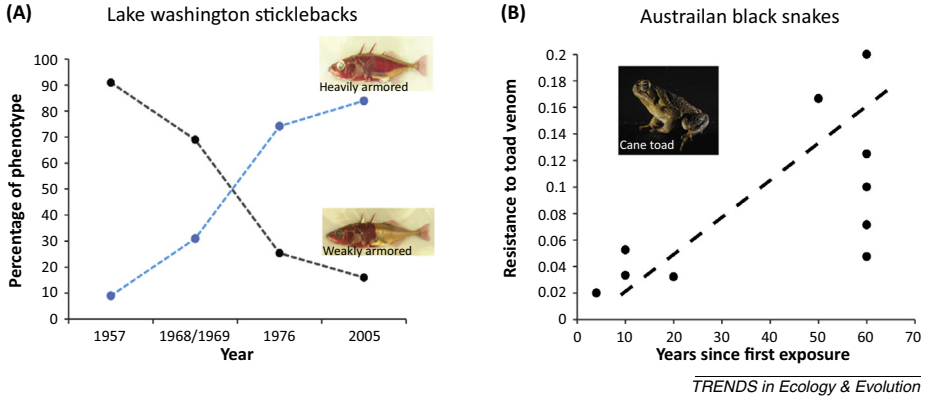

Figure I. Phenotypic time series of stickleback armoring and snake resistance to toad venom.

populations showed an immediate decline in mean fitness and subsequent rebound with increasing frequency of selfing-efficient genotypes. However, the environmental shift was not sufficiently harsh to provide a full test of evolutionary rescue because pollinator loss did not lead to negative growth.

Summary and next steps: toward tighter integration of theory and laboratory studies

Theory and laboratory studies have each identified factors contributing to the likelihood of evolutionary rescue that have yet to be explored using the alternative approach (see side-by-side comparison in Table 1). For example, theoretical studies highlight the importance of duration of time at low abundances and competition, but these factors remain to be explored in a laboratory setting (Table 1). More generally, tighter integration of theory and laboratory studies could be achieved through the development of realistic evolutionary demographic models for laboratory systems.

Evolutionary rescue in nature

Given the recent proliferation of studies documenting adaptive evolution in only a few generations [49], one might predict that clear examples of evolutionary rescue would be abundant in wild systems. Although examples exist (evolved acid tolerance of *Chlorella* phytoplankton in Canadian lakes impacted by industrial pollution [16], antivitamin K resistance in rats, and rescue from biological control in rabbits [12]) we conclude, along with [16] and [7], that a clear signature of evolutionary rescue in nature is rare. This probably stems from indeterminate effects of species interactions on population growth, a focus on single rather than multiple correlated fitness traits, confounded effects of dispersal, and density-dependent processes that can mask adaptive evolutionary responses [7,16,50]. Despite these complications, we highlight previously unrecognized candidate examples where evolutionary rescue has potentially acted as an ally for declining populations (Box 2) or led to the evolution of resistance in species that threaten human welfare (Box 3). As is often the case, demographic data are missing in these examples

Box 3. Evolutionary rescue as a threat to human welfare

Although evolutionary rescue has often been portrayed in the context of conservation biology as a potential mechanism by which species of concern can avoid extirpation, evolutionary rescue is also a mechanism by which deleterious bacterial and insect species persist in the presence of medical or agricultural treatments designed to limit their spread. Here we highlight examples of trends in resistance that exemplify the phenotypic response to selection expected during evolutionary rescue, in bacterial (Figure I) and arthropod (Figure II) taxa.

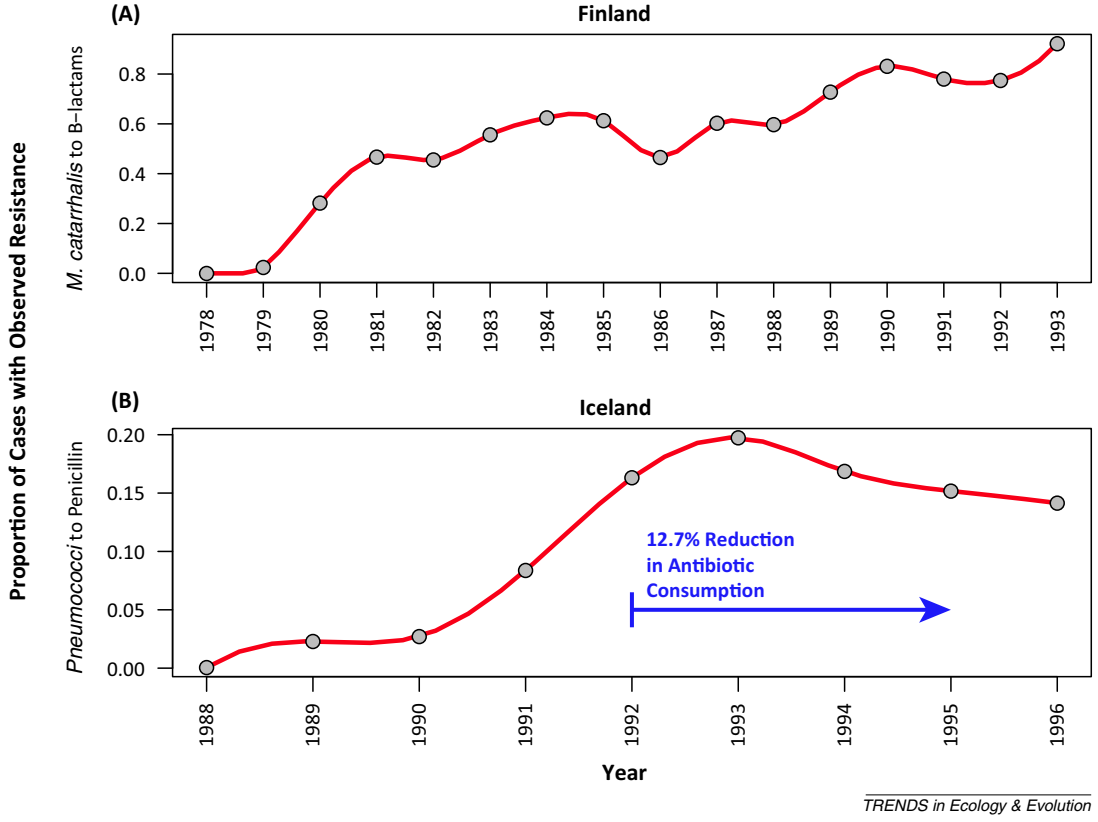

Figure I. Antibiotic resistance in bacteria from **(A)** Finland and **(B)** Iceland. Resistance has arisen repeatedly in a wide range of bacterial taxa in response to the use of several antibiotic compounds intended to control their abundance. Increasing resistance is an example of adaptive evolution in bacterial populations resulting from selection imposed by the use of antibiotics, allowing bacteria to persist. Increasing observations of resistance by *Moraxella catarrhalis* to β-lactams in clinical settings in Finland over time exemplify the phenotypic response characterizing evolutionary rescue (top). Observations of increasing rates of resistance by Gram-positive pneumococci bacteria to the antibiotic penicillin over time follow the phenotypic trend expected under an evolutionary rescue scenario, with a decrease in resistance observed following relaxation of selection in the form of a 12.7% reduction in antibiotic consumption in 1992 (bottom). Reproduced, with permission, from [83].

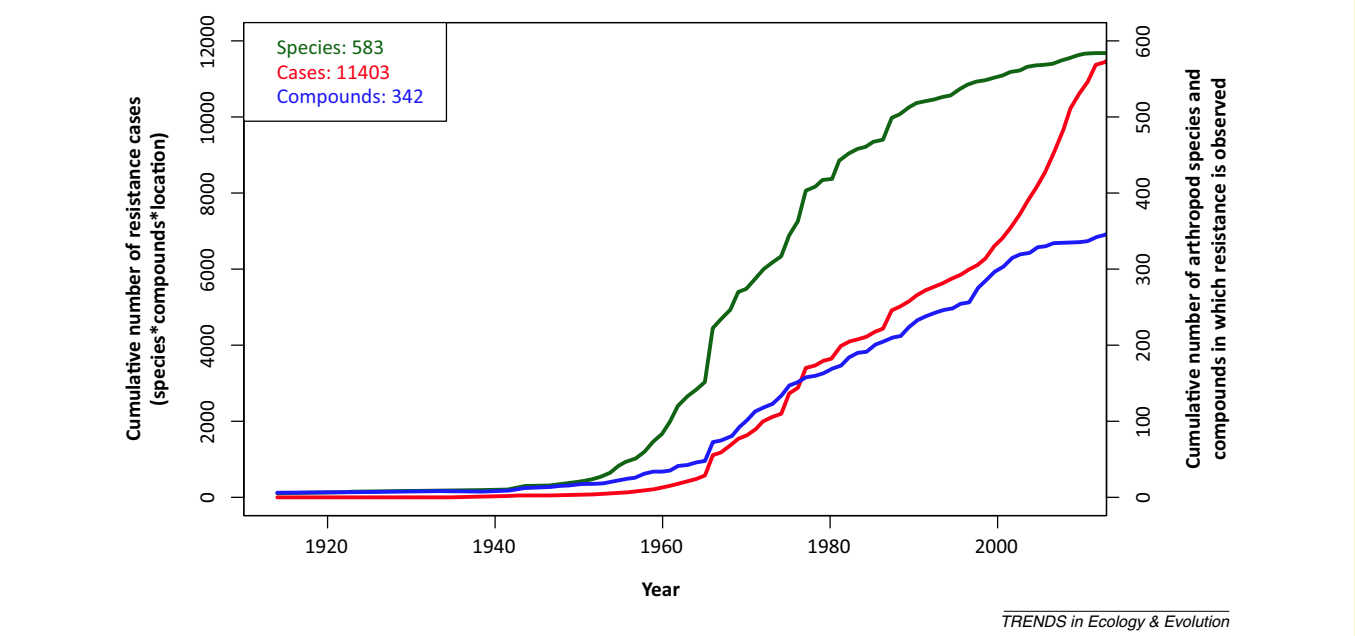

Figure II. Insecticide resistance in arthropods. Evolutionary rescue and the rise of resistance in agricultural pests. Since the early 1960s, the occurrence of arthropod resistance to agricultural pesticides has increased significantly. By 2013, 11 403 cases of arthropod resistance (red line) had been recorded in the USA, with members of 583 species (green line) exhibiting resistance to more than 342 pesticide compounds (blue line). Evolutionary rescue is likely to be responsible for the ability of these arthropod species to persist in the face of the strong environmental stress imposed by the use of pesticides to control their abundance, incurring a significant economic cost manifesting as lost production of food and other agricultural products. Reproduced from [84].

(Boxes 2 and 3), making it unclear whether the populations showed the hallmark U-shaped demographic trajectory. By contrast, we highlight two putative examples of evolutionary rescue where both demographic and adaptive phenotypic evidence are available (Box 4).

These rare examples serve to reinforce the pressing need for research that operates at the interface between ecology and evolution [51,52], because the current paradigm that disconnects population dynamics from evolutionary dynamics impedes our ability to detect and diagnose evolutionary rescue. Indeed, research on eco-evolutionary dynamics has provided compelling evidence of linkages between evolutionary change and population dynamics [17,53–55]. It is necessary for future research to encompass a wide range of environmental conditions such that extinction events become part of the picture. This need also underscores the value of long-term biological monitoring of both population demography and heritable traits influencing fitness, a combination well poised to explore evolutionary rescue in nature.

Future directions

Although our understanding of the factors facilitating evolutionary rescue has increased considerably in recent years, there remains considerable scope for further advances. In this section, we scan the horizon for where the field might develop and suggest areas of potential application.

What are the long-term consequences of short-term rescue?

Our review provides several putative examples of evolutionary rescue outside the laboratory (Boxes 2–4) but only time will tell whether these populations remain viable over longer timescales. For example, does short-term rescue render populations less likely to adapt to a new stressor in the future? This is particularly relevant for populations where evolutionary rescue has led to the fixation of adaptive alleles and ostensibly reduced standing genetic variation, thus reducing the potential for future rescue. Environmental stressors might also shift phenotypic distributions in one direction thereby restoring positive population growth in the short term, but the erosion of genetic and phenotypic diversity might have longer-term consequences that leave populations vulnerable to extinction. In this way selection and evolutionary rescue could lead to an evolutionary trap, if the population adapts to new conditions but is maladapted to alternative future conditions.

What is the role of dispersal in evolutionary rescue?

Exploring evolutionary rescue within a metapopulation context shifts the focus away from within-population processes to consider the influence of dispersal from other populations. Dispersal potentially influences the probability of evolutionary rescue in several ways (Box 1), but this has rarely been studied experimentally [9,45] and never in sexual species. Dispersal in the form of immigration has two main effects: it increases genetic diversity and increases population size. Increased population size should then lead to an increased rate of mutation of beneficial alleles [31]. However, one of the complications with dispersal is the interplay with density dependence. Under positive density dependence, absolute fitness will increase with increased population size, suggesting that immigration will enhance evolutionary rescue. By contrast, with negative density dependence, dispersal to a sink population might impede adaptation and evolutionary rescue (e.g., [4]). Theoretical studies have also highlighted the potential for dispersal of sexual species to erode local adaptation through migration load [32]. Understanding

Box 4. Elusive evidence of evolutionary rescue in nature

Here we highlight two case studies that suggest evolutionary rescue in nature: evolved resistance to a novel pathogen by rainbow trout (*Oncorhynchus mykiss*); and evolution of an adaptive silent morphology by field crickets (*Teleogryllus oceanicus*) following introduction of a parasite. Whirling disease (*Myxobolus cerebralis*) has wreaked havoc on naïve populations of North American salmonids and has been implicated in the decline of multiple populations of trout [85]. Whirling disease, which is transmitted via parasitic 'TAM' spores, selectively affects the juvenile life stages through the degradation of cartilaginous tissues, culminating in catastrophic skeletal deformities leading to the characteristic 'whirling' swimming behavior and death. In 1995, whirling disease was detected in a trout population from Montana, USA [86]. In only five breeding seasons, the number of spawning recruits to the population declined from 60 individuals to almost zero, followed by a slow recovery. Coinciding with recovery, experimental evidence reported in [86] confirmed heightened resistance to the effects of whirling disease by the progeny of younger compared with older cohorts (Figure IA). The acoustically orienting invasive parasitoid fly (*Ormia ochracea*) has apparently driven the evolution of an adaptive silent morphology in male field crickets on the Hawaiian island of Kauai. The auditory sexual signal of male crickets, used to attract females, is produced by males with 'normal' wing morphology including the stridulatory apparatus of a file and scraper that enable sound production. This sexual signal also attracts gravid parasitoid flies that deposit larvae on male crickets, ultimately leading to their death. Zuk and colleagues [87] documented a steep population decline over 10 years of study and only a single calling male was observed in 2001. By 2003 the population was apparently rebounding (Figure IB); however, instead of normal wing morphology, the researchers encountered abundant but silent males. On closer examination, they found that nearly all males had female-like wings ('flatwings') that lack the wing structures to produce song [87]. They report that a mutation invaded the Kauai cricket population in 12–20 generations and occurred on a single gene [88]. Figure IA adapted, with permission, from Figures 1 and 2 in [86]; Figure IB adapted, with permission, from Supplement 1 in [3]. Percentage flatwing line styled with guidance from M. Zuk and J. Rotenberry. Photograph credits: V. Blazer (spore), S. Hallett (trout), and R. Tinghitella (crickets).

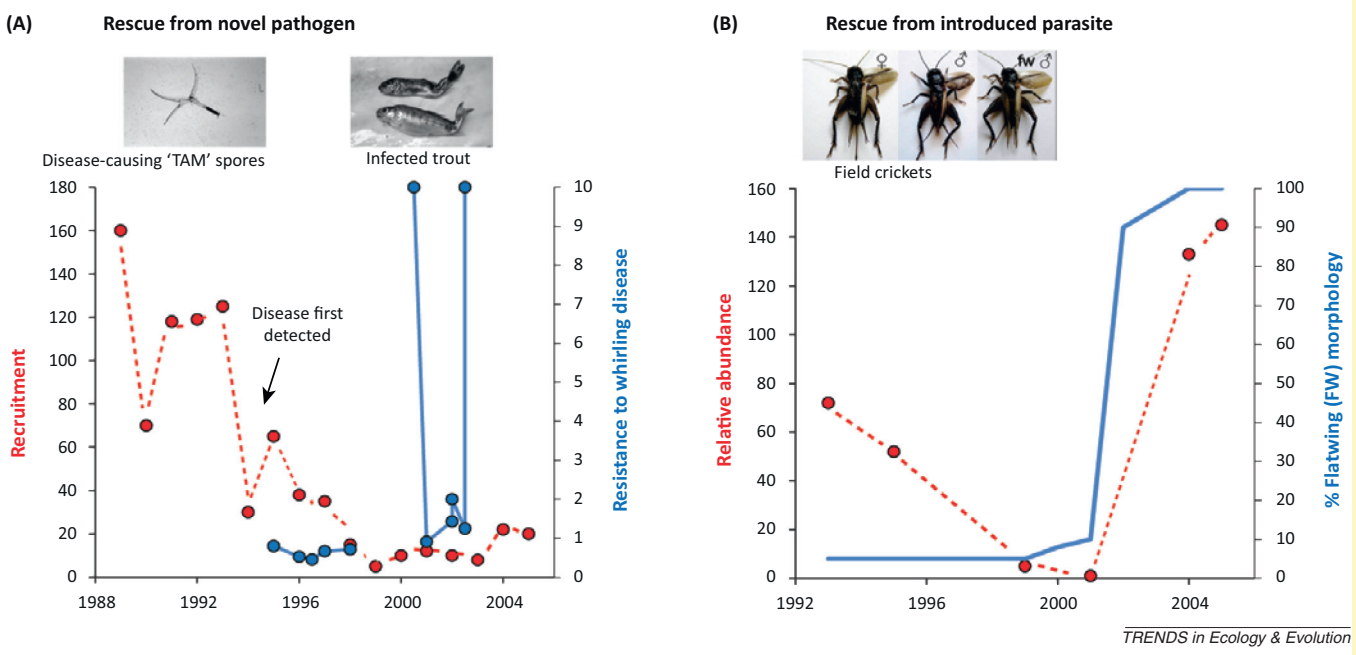

Figure I. Time series of demography and adaptive response in rainbow trout and field crickets.

the conditions when dispersal reduces or enhances the opportunity for adaptation and evolutionary rescue is a prime target for future study [30,56].

Demographic, genetic, and evolutionary rescue: how do these interact?

Understanding the relative importance of demographic rescue, genetic rescue, and evolutionary rescue in rescuing populations with different life histories (e.g., short versus long generation times) and dispersal capacities will be a critical step for informing real-world management. Organisms withstand environmental change and spread risk in different ways, including movement (often large, long-lived vertebrates), plasticity, life-history diversity such as resting stages (e.g., seed or egg banks), and adaptive evolutionary change [57]. It is possible that standing genetic variation, adaptive phenotypic plasticity, or corridors that preserve the ability to disperse might be relatively more important for organisms with long versus short lifespans. To the extent that this is true, management options for long-lived and isolated populations might include assisted migration to facilitate gene flow, whereas such actions might be less important for organisms with shorter generation times.

Applications

Application of the principles of evolutionary rescue necessitates a shift in focus, from asking can adaptive evolution save declining populations in the wild, to what combination of factors maximizes the likelihood of rescue (e.g., [58])? To this end, our synthesis of factors influencing the probability of evolutionary rescue (summarized in Table 1) is intended to guide 'evolutionarily enlightened' management and conservation planning [11,59]. We expect the principles governing evolutionary rescue potential will be of practical use in the context of ocean acidification [60,61], increasing global temperatures [62], biological invasions [50,63–65], and the rise of antimicrobial resistance to antibiotics, which the World Health Organization

(WHO) has recently highlighted as a global problem [WHO (2014) *Antimicrobial Resistance: Global Report on Surveillance* (http://www.who.int/drugresistance/documents/surveillancereport/en/)]. It remains unclear, however, whether certain types of environmental change (e.g., salt stress versus thermal stress) are inherently more difficult to surmount through evolutionary rescue, and this is ripe for future work. By formalizing the role of evolutionary rescue within the conservation toolbox, we take an important step toward addressing the question of which populations might be capable of adapting quickly enough to outpace environmental change and avoid extinction and which factors can be managed to enhance the likelihood of evolutionary rescue.

Although we have emphasized the potential for evolutionary rescue in conservation, evolutionary rescue can also impact human welfare through its effect on food security and through the rise of drug-resistant disease vectors and pathogens (Box 3), among other pathways. Evolutionary rescue of insect-pest populations resulting from selection for resistance to insecticides represents a US$2–7 billion annual loss in crop production, with the cost of developing a new insecticide estimated at a minimum of US$80 million in 1999 [66]. In clinical settings, evolutionary rescue of bacterial populations and disease vectors has consequences for human health [WHO (2014) *Antimicrobial Resistance: Global Report on Surveillance* (http://www.who.int/drugresistance/documents/surveillancereport/en/)] [67]. Dichlorodiphenyltrichloroethane (DDT) resistance in mosquitoes has significantly inhibited global attempts to control malaria, permitting the continued occurrence of an estimated 300–500 million cases [68] and 3 million deaths each year [69]. In these contexts, management will instead aim to diminish the capacity for evolutionary rescue, possibly by increasing the rate and direction of environmental change (e.g., increasing the rates and types of insecticide applied) [50]. Encouragingly, substantial efforts to confront the malicious evolution of pathogens with evolutionary principles are already gaining momentum in the field of medicine [70].

Concluding remarks

Much work has been done to increase our understanding of the factors contributing to evolutionary rescue. Theoretical studies confirm that demographic, genetic, and extrinsic factors are determinants of evolutionary rescue and several of these have been explored in the laboratory (Table 1). There is unequivocal evidence that populations are most likely to be rescued when the initial population size is large, initial standing genetic variation is high, and environmental change is gradual. Moreover, theory suggests that organisms with longer generation times are the least likely to be saved by evolution [12]. This is a cause for concern because many examples of evolution rescuing pest populations emerged from systems characterized by fast generation times. Ultimately, it remains to be seen whether evolutionary rescue is more often the villain or the hero in conservation.

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