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Review

Recognizing adaptation costs in the Anthropocene

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While populations can adapt to rapid environmental change in the Anthropocene, adaptation costs may limit evolutionary rescue, even when standing population genetic variation is high. Here, we argue that adaptation costs are linked to evolutionary trade-offs involving scenario- or system-specific traits that usually promote environmental specialization and species coexistence. Adaptation costs can be cryptic, and are more likely to emerge in populations under fluctuating environments or under multiple stressors. Adaptation costs mediated by ecological processes such as competition and symbiosis can limit population growth and species ranges. We advocate for considering adaptation costs in global change studies to improve predictions of future population responses, biological production, and ecosystem resilience.

Highlights

Efforts to understand limits on evolutionary rescue in response to rapid environmental change have emphasized adaptation constraints, but adaptation costs are often overlooked.

A growing number of studies have shown that adaptation costs are common and can limit evolutionary rescue, impeding population/species conservation efforts.

A failure to account for adaptation costs can lead to inaccurate and potentially overly optimistic predictions of population resilience.

Quantifying and incorporating adaptation costs into evolutionary rescue models would improve predictions of responses of populations to rapid global change.

Why should we consider adaptation costs in the Anthropocene?

Global change is causing rapid environmental impacts that are threatening biodiversity and disrupting ecosystems because of factors such as rising temperature, ocean acidification, and salinity change [1–5], among myriad others. Given these impacts, two fundamental questions are (i) how will the biota respond to rapid global change? and (ii) will populations disappear or adapt in geographic areas most severely impacted by global change pressures? **Rapid adaptation** (see Glossary) via natural selection can increase **absolute fitness** in the face of environmental stress such that populations are more likely to persist, a process called **evolutionary rescue** [6–9].

Adaptation costs are ecoevolutionary processes that limit the extent of evolutionary rescue and manifest as reduction of an adapted population's fitness in ancestral conditions relative to ancestral lineages [10–13]. Adaptation costs can be caused by **evolutionary trade-offs** in alternative environments [14] (Figure 1). We focus primarily on adaptation costs involving evolutionary trade-offs, which occur when a gain in fitness or trait performance in one environment results in the decline of fitness or trait performance of an alternate trait in another environment [15]. Adaptation costs can arise from trade-offs that involve traits leading to specialization in new environments (i.e., niche differentiation [16]). Idiosyncrasies in these trade-offs can result from evolutionary or adaptive history that cause certain traits to be better selective targets [11,13,17]. This is especially relevant for populations adapted to fluctuating environments due to strong seasonality or migration. In fact, empirical demonstrations of evolutionary rescue in fluctuating environments often show slowed or limited adaptation [18,19]. Considering how trade-offs and resulting adaptation costs impact the likelihood of adaptation is crucial for generating accurate models and predictions of evolutionary rescue, because increasing environmental variability is expected with global change. Which of these trade-offs are important will depend on the particular populations and the ecological context. Ignoring these adaptation costs in the context of anthropogenic global change could yield falsely encouraging predictions of resilience based on observed trait shifts responding to environmental change. Several studies have examined trade-offs in fitness-related traits that arise following

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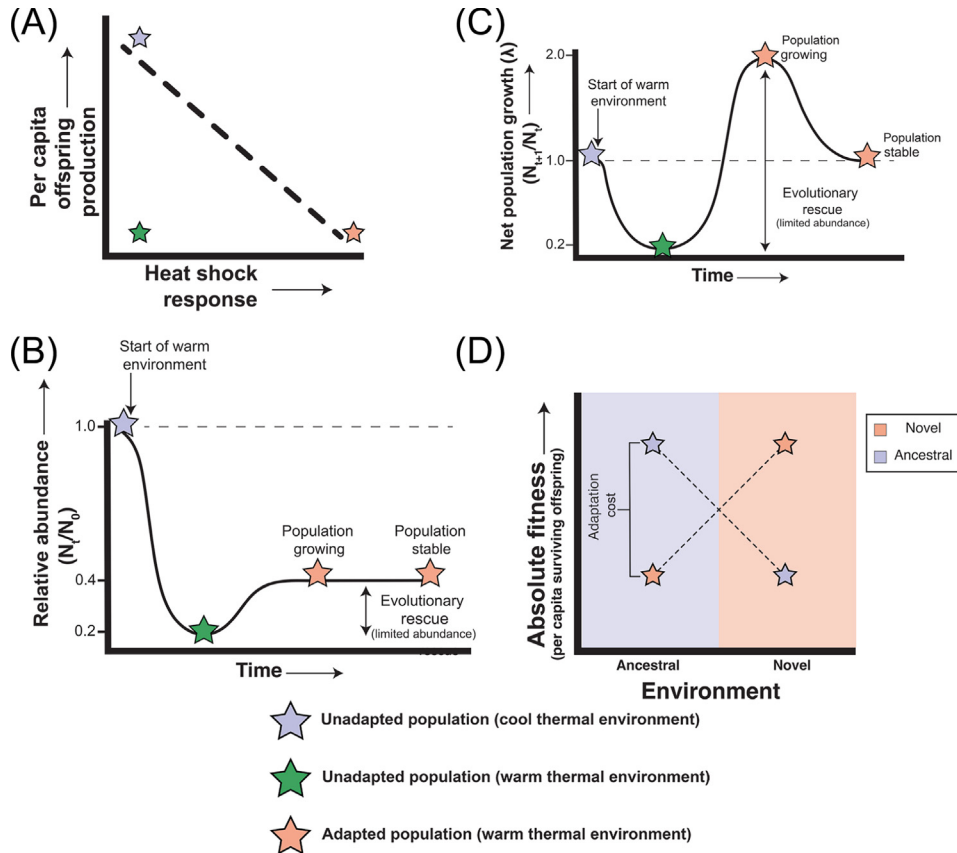
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Figure 1. Adaptation with costs because of trade-offs. Colored stars (bottom legend) indicate an unadapted population in cool, ancestral environments (blue); an unadapted population in a warm, novel environment (green); and an adapted population in a warm, novel environment (pink). (A) The trade-off relationship between per capita offspring production and heat-shock response. (B) Changes in population abundance [relative to the starting (blue) generation]. Evolutionary rescue recovers population abundance to a fraction of the ancestral generation level. The relative abundance of the adapted (pink) population here reaches a plateau after recovery. (C) The observed net population growth (λ; N_{t+1}/N_t) for three sequential generations adapting to temperature changes where each generation has the same generation time. The net population growth of the warm (pink) generation is higher than the cool (blue) population because λ is estimated on the basis of abundance measures of the preceding (green) generation, not the initial (blue) generation. (D)The test of adaptation costs. Costs of adaptation are inferred if the fitness of the adapted (pink) population declines when experiencing ancestral foreign (blue) environments.

adaptation to anthropogenic change and have quantified adaptation costs in alternative environments [20–24]. However, specific measurements of adaptation costs and the trade-offs involved have rarely been incorporated into projections of population persistence and extinction during anthropogenic change (but see [25]).

For a theoretical example of how trade-offs can limit fitness and reveal costs, consider the example of a temperate population of high-altitude insects whose environment warms to resemble the low-lying valleys beneath (Figure 1). High-altitude adaptation can lead to large flight muscles that maintain flight in low-pressure air systems, which have the added benefit of maintaining body temperature due to excess energy produced by wing flapping. Thus, the need for metabolic pathways to regulate temperature or protect against thermal stress is decreased. This gives the temperate, high-altitude population more energy to produce more offspring. But as the environment

warms at high altitudes, the insects now experience extra-high temperatures because of their continued need to use highly developed flight muscles in low-pressure air systems. Added heat stress can cause excess energy reserves to be diverted toward increasing somatic maintenance (e.g., heat-shock response) and subsequently reduced energy allocated for offspring production. This shift represents two potential consequences: (i) limited adaptation with lower population abundance and (ii) a **fitness trade-off** with reduced maximum population growth in previously benign environments. Both cases result from environmentally mediated physiology driven by selection for particular phenotypes and trade-offs.

Adaptation costs and **adaptation constraints** are not mutually exclusive, because they can both restrict population growth and persistence and limit evolutionary rescue [10,12,14,26–28]. Adaptation constraints may prevent adaptation by natural selection because of insufficient genetic variation, **antagonistic pleiotropy**, selection on correlated traits, linkage with maladapted alleles, or from Haldane's demographic **cost of natural selection**. Under the latter, genetic variation is reduced too quickly for new beneficial mutations to arise, making it more difficult to adapt to new environments [29,30]. Adaptation constraints have been widely studied (reviewed in [28,31,32]) and are not the main focus of this review.

Recent studies on evolutionary rescue have focused on the evidence for rescue, how to identify evolutionary rescue from genetic and demographic rescue, and constraints on evolutionary rescue [8,28,33]. But these studies have paid relatively little attention to adaptation costs and their consequences for evolutionary rescue, particularly in terms of the trade-offs involved or when adaptation costs are likely to appear. Hence, the goals here are to (i) briefly discuss causes and examples of adaptation costs, (ii) discuss implications of adaptation costs for evolutionary rescue and population persistence, and (iii) suggest future approaches for analyzing adaptation costs and advocate for their inclusion in global change studies.

Evidence and relevance of adaptation costs

The extent of adaptation and adaptation costs in different environments can be measured experimentally by comparing the fitness of both the adapted and ancestral populations in both the novel and ancestral environments under common garden conditions and/or in reciprocal transplant environments [12] (Figure 1D). An increase in absolute fitness of the adapted population relative to the ancestral population in the novel environment would indicate adaptation to the novel conditions. At the same time, a reduction in absolute fitness in the adapted population relative to the ancestral population in the ancestral environment would indicate adaptation costs (Figure 1D) [10–13]. Sometimes adaptation costs can be cryptic and are revealed in the presence of additional stressors in the ancestral environment [34]. In addition to potentially limiting evolutionary rescue, adaptation costs are problematic for conservation efforts, given that a population experiencing costs will have lower absolute fitness if the environment is restored to its ancestral condition.

An adaptation cost and limited evolutionary rescue in the context of rapidly induced anthropogenic environmental change is illustrated by studies of single-celled phytoplankton under ocean acidification conditions [35,36]. In the coccolithophorid *Gephyrocapsa huxleyi*, laboratory selection at high CO_2 revealed the ability to adapt to high CO_2 levels, leading to higher growth rate and shell production rate (calcification) relative to control lines reared at low CO_2 when assayed under high CO_2 conditions [35,36]. However, an adaptation cost was revealed when the high CO_2 lines showed lower growth rates than the low CO_2 lines when both were grown in low CO_2 conditions. In addition, adaptation was limited: laboratory selection at high CO_2 after 500 and 2100 generations was insufficient to fully restore growth rates at high CO_2 to comparable values found under low CO_2 conditions [35,36].

Glossary

Absolute fitness: the number of surviving offspring produced by an individual or genotype within a discrete, nonoverlapping generation.

Adaptation constraints: genetic and/or environmental processes that prevent adaptation from proceeding, including insufficient genetic variation, antagonistic pleiotropy, selection on correlated traits, linkage with maladapted alleles, or from Haldane's demographic cost of natural selection.

Adaptation costs: a fitness decrease of an adapted population relative to that of an ancestral population when transplanted to the ancestral environment. Adaptation costs arise from trade-offs and can limit the rates of population growth after adaptation takes place.

Antagonistic pleiotropy: when a single gene encodes multiple traits such that some of the traits increase fitness in one environment or life-history stage, whereas others reduce fitness of the same population in an alternate environment or life-history stage. Antagonistic pleiotropy is one of several possible genetic mechanisms that could contribute to fitness trade-offs.

Anthropocene: the proposed current geological period during which human activity has been a dominant influence on environmental change.

Compensatory adaptations: fixation (or increase in frequency) of beneficial mutations that reduce the deleterious effects of previous mutations fixed either by drift or by pleiotropy.

Cost of natural selection: a demographic consequence of natural selection whereby individuals with deleterious alleles are eliminated from a population leading to lowered reproductive capacity and reduced population abundance.

Evolutionary rescue: the process by which a population undergoing initial decline following exposure to stress avoids extinction by adaptation via natural selection.

Evolutionary trade-off: a gain in fitness or trait performance in one environment or situation that results in the decline of fitness or trait performance of an alternate trait in another environment. Evolutionary trade-offs can arise through several, although not mutually exclusive, mechanisms. Finite resource allocation prevents two fitness-related traits from being optimized

The evolution of pesticide resistance in many species frequently results in adaptation costs. Sixty percent of 170 studies of insecticide resistance involving transplant to ancestral environments found adaptation costs across numerous insect species [34]. The evolution of pesticide resistance might involve mutations or gene duplications of the pesticide target, such as ion channels or acetylcholinesterase, or increased expression of detoxification enzymes (e.g., cytochrome P450s) that neutralize the pesticides. These adaptations, however, often entail trade-offs, such as lowered fecundity, mating success, or energetic reserves in exchange for increased pesticide detoxification, that lead to reduced absolute fitness in their ancestral, pesticide-free environment [34]. Moreover, when insecticide-resistant populations are exposed to novel environments (e.g., environments with modified temperature) in addition to their ancestral environments, further fitness trade-offs are observed [34]. Thus, in many cases, adaptation costs are present across environments, such that pesticide resistance is beneficial when pesticides are present but leads to lower fitness in the absence of pesticide (ancestral environment) and in novel environments.

Adaptation costs are not always evident or immutable [37]. For example, **phenotypic plasticity** can maintain absolute fitness across environments [38]. Likewise, fitness-related traits can be positively correlated, leading to increased absolute fitness when populations experience novel temperatures [39]. Additionally, over longer periods of time, **compensatory adaptations** can fully restore absolute fitness [40–42]. For instance, resistance to organophosphate insecticides in the mosquito *Culex pipiens* first involved a major resistance allele that entailed adaptation costs. But additional mutations mitigated the adaptation costs over a 40-year period [43].

Trade-offs associated with adaptation costs are often species- or scenario-specific

Here, we are interested in trade-offs in fitness-related traits that arise following adaptation to new environments, including the evolution of specialization, niche breadth, and range limits [14]. Evolutionary trade-offs can arise through several, though non–mutually exclusive, mechanisms, including antagonistic pleiotropy, energetic constraints (finite resource allocation), and functional constraints [15]. Such trade-offs often require additional adaptation (e.g., compensatory mutations and/or recombination and further selection) to restore the fitness of the population to ancestral population levels and achieve full evolutionary rescue [42,44]. Fitness trade-offs are a type of evolutionary trade-off where a fitness gain in one environment or situation results in a fitness decline in another environment [15]. Simply showing a negative trait correlation is not sufficient to demonstrate a trade-off. Negative trait correlations can result from correlational selection for particular trait combinations [45] or from trait-specific selection that promotes genetic polymorphisms [46], and both of these mechanisms can cause traits to be negatively correlated without an observable fitness penalty. Therefore, demonstrating a fitness effect is essential when identifying a fitness trade-off.

Identifying trade-offs that lead to adaptation costs involves in-depth studies on which traits affect population growth in particular environmental contexts. These trade-offs impact food web structure and global productivity by shaping biodiversity and demography, often in species- or scenario-specific ways. Some classic trade-offs are offspring number versus size, growth versus reproduction, and current reproduction versus future survival [47]. Environmental change alters selection pressures, shifts the traits involved in a trade-off, and changes the degree to which those traits contribute to population growth. While trade-offs affect population growth and estimates of population persistence, they are not universal and can be species-specific [48]. Some conditions may select for smaller body size, shorter generation time, and faster population growth (e.g., [49]), whereas others may favor larger body size, shortened generation time, and slower population growth (e.g., [50]). Importantly, selection pressures and environmental impacts

simultaneously, and their combination is optimized instead. There can also be functional (physical and/or structural) constraints, such that features that enhance performance of one task can decrease performance of another, such as force–velocity trade-offs related to muscle fiber type composition. Evolutionary trade-offs could also result from antagonistic pleiotropy or conditional neutrality.

Fitness trade-off: a type of evolutionary trade-off, where absolute fitness gain in one environment or situation results in fitness decline in another environment or situation. A fitness trade-off in alternative environments could arise from many different mechanisms, such as antagonistic pleiotropy, limited energetic resources, or physical or functional constraints.

Maladaptation: deviation from the trait optimum of a population with negative impacts on the fitness of a population.

Phenotypic plasticity: the ability of a genotype to express different phenotypes in response to environmental conditions during development or as a short-term acclimation response. Plastic phenotypes can include morphological, behavioral, and physiological traits.

Rapid adaptation: fitness improvements via natural selection over fewer generations than expected on the basis of the pace of environmental change.

often vary throughout the year, adding complexity to life-history evolution and the evolution of trade-offs [51].

An example of adaptation costs involving trade-offs comes from populations of the copepod *Eurytemora affinis* species complex that have invaded freshwater habitats from ancestral saline habitats within the past century [52,53]. Under common garden conditions, the freshwater populations show greater survival relative to ancestral saline populations under freshwater conditions, indicating adaptation of the former to freshwater conditions [20]. However, adaptation costs are apparent when comparing the freshwater and saline populations under ancestral saline conditions, where the freshwater population shows reduced survival relative to its saline ancestor. The loss in high-salinity tolerance and gain in freshwater tolerance in the freshwater population indicates evolutionary trade-offs between high- and low-salinity environments. The negative genetic correlations between survival in freshwater versus higher salinities support the existence of these fitness trade-offs. Moreover, because of the high energetic costs of ion uptake required to survive under freshwater conditions, freshwater survival results in longer development time and lower egg production in the freshwater populations relative to saline populations in their native saline habitat. The energetic cost is apparent in the high food consumption required by the freshwater population to survive under freshwater conditions [54]. In this case, both the high energetic costs of living in the novel environment and the trade-offs in physiological function between habitats are important to consider when examining the costs of adaptation to changing environments.

Trade-offs leading to adaptation costs may also manifest only under ecological interactions. For instance, increased tolerance or performance in a new environment could lead to adaptation costs in terms of reduced competitive ability in coexisting populations. Tide pool systems represent classic examples of wide temperature fluctuations, which expose populations to thermal stress. Because of their isolation, there is intense interspecific competition in tide pools. In a latitudinal study of the tide pool copepod *Tigriopus californicus*, populations that faced the greatest thermal stress displayed the strongest high-temperature stress tolerance. However, high-temperature–adapted populations were less likely to survive to adulthood at more moderate ancestral temperatures when competing with low-temperature populations [55]. A similar competitive disadvantage of lowered survival was shown for populations of the water flea *Daphnia magna* that had adapted to warming relative to those that had not [56]. This reduced competitive advantage of thermal tolerant phenotypes represents a cryptic cost of adaptation revealed only under species interaction. Thus, the context of traits involved in adaptation costs might not always be obvious. Overall, examples of trade-offs that lead to adaptation costs can involve idiosyncratic responses even among common fitness-related traits in systems experiencing similar environmental stressors leading to differential evolutionary consequences for species adapting to global change.

Adaptation costs in response to multiple stressors

Global change exposes populations to multiple environmental stressors that can interact in complex ways. Importantly, adaptation costs and trade-offs are more likely to arise when multiple stressors interact than under single stressors [57–61], because organisms face greater physiological stress [62] and because of increased dimensionality of divergent selection [63]. Accounting for the synergistic and antagonistic effects of combined stressors can provide more accurate estimates of population growth and persistence than accounting only for single stressors [62].

The complex effects of multiple stressors on adaptation and its costs are rarely tested experimentally [57–61]. Some examples of adaptation costs linked to multistressor global change and driven by trade-offs include the copepods *Acartia tonsa* and *A. hudsonica* that adapt to combined ocean warming and acidification (OWA) [57–60]. For both species, adaptation costs and

constraints are experimentally demonstrated, with notable decreases in absolute fitness and phenotypic performance under OWA relative to either warming or acidification alone. In these cases, trade-offs between different life-history traits lead to adaptation costs not evident under single stressors, even though population genetic variation was maintained [58,64]. Moreover, adaptation of *A. tonsa* to OWA includes loss of thermal tolerance and developmental phenotypic plasticity [57] that leads to adaptation costs when the OWA lineage is exposed to its ancestral benign temperature and pH environment. Likewise, the OWA lineage fares worse in its ancestral environments under food limitation than the ancestral lineages [59]. There remains a significant gap in our understanding of the effects of multiple stressors on adaptation, adaptation costs, and evolutionary rescue. Such a gap must be closed before we can confidently make predictions of population persistence in the **Anthropocene**.

Ecological consequences of adaptation costs

Adaptation costs can impact population demography, species interactions, food web structure, and ecosystem productivity. For instance, copepods that have evolved tolerance to toxic dinoflagellates [65] experience trade-offs between fecundity and longevity [66] that prevent toxin-tolerant genotypes from becoming fixed at the population level. When toxic algal blooms wane, the toxin-tolerant copepods exhibit an adaptation cost and decline in abundance, allowing toxin-susceptible copepods to dominate. This case resembles the dynamics of insecticide tolerance mentioned earlier. Additionally, fitness restrictions limit species ranges and can promote niche differentiation by reducing either competition or spatial overlap between predator and prey at the range boundaries [67–69]. For example, fitness trade-offs in foreign environments for the monkeyflowers *Mimulus cardinalis* and *M. lewisii* prevent growth outside of their adapted environments [69]. These fitness trade-offs are explained by trade-offs in flowering time versus photosynthetic capacity. The trade-offs determine range limits and help establish the appropriate niche for these monkeyflower species. In other plants, trade-offs across life stages impact range shifts caused by climate change [70]. Specific trade-offs, such as seed number versus seed size, lead to either increased colonization potential or increased probability that species go extinct locally. These examples demonstrate how adaptation costs can determine species interactions across trophic levels and across ranges with species or scenario-specific trade-offs.

Adaptation costs are also evident in mutually coadapted species. Mutualistic coadaptation selects for maximal fitness in both a host and its symbiont to the point where their separation, or the introduction of a new symbiont, reveals fitness costs or negative physiological consequences. For example, cnidarians colonized with non-native endosymbionts exhibit lower carbohydrate metabolism, which can reduce their capacity for growth [71]. Compensatory adaptation, however, can recover these initial costs [72] and has been demonstrated in host–symbiont partner-switch experiments [73]. Geographic origin can also determine fitness impacts of symbiosis and subsequent adaptation costs. Plants will experience fitness costs when their arbuscular mycorrhizal fungal symbionts and soil in which plants are grown originate from foreign locations [74]. Thus, constraints and fitness costs can be revealed when symbionts are removed or changed from coadapted species.

Species interactions can limit adaptation. During temperature-dependent competition, adaptation can lead to microhabitat niche differentiation that maintains species coexistence, but at the cost of population growth rates [75]. Thus, competition and biotic interactions during adaptation can have complex interactions that might promote ecosystem stability at the cost of population growth and absolute fitness. To this point, few studies have attempted to account for ecosystem effects of adaptation, its costs or constraints, and how these factors may affect – or be affected by – species interactions. Hence, the impact of adaptation costs on species interactions is a major gap in our understanding of evolutionary rescue in the Anthropocene.

Future considerations for studying adaptation costs

Because adaptation may not fully rescue populations [28], future studies need to identify adaptation costs to improve predictions of evolutionary rescue. This involves observing fitness costs and trade-offs after rapid adaptation to environmental change takes place, particularly in fluctuating environments. Studies that consider both the magnitude of environmental fluctuations and their predictability relative to the timescale of the organism's life-history traits are likely to be more useful [76]. We can also further explore the effects of complex stressor interactions on adaptation costs leading to ecological consequences that can impact species distributions and interactions. Here, we recommend some approaches that could help direct the evaluation of adaptation costs and trade-offs.

The empirical measurements of adaptation costs, such as those described above, can be input into demographic models to determine population growth and persistence in the face of global change, especially in situations where frequently fluctuating environments are common. As populations adapt to novel environments, the reduction in fitness due to adaptation costs will impede the extent of population recovery. With the presence of prolonged stressful conditions due to anthropogenic change, the demographic costs might be severe, with populations experiencing costs of adaptation over extended periods of time in novel environments. Thus, it is important to accurately quantify the adaptation costs in order to make more accurate projections on the probability that populations will survive the climate crisis.

In systems where multigeneration selection experiments are possible, changing fitness patterns across environments (e.g., reciprocal transplant experiments) and across generations (e.g., experimental evolution studies) can reveal fitness trade-offs and adaptation costs [77,78]. These same methods are difficult to apply to long-lived organisms or among organisms where absolute fitness is challenging to measure (e.g., trees, large vertebrates). Instead, one can employ modeling approaches, which can integrate somatic growth and molecular marker data to improve spatial distribution forecasts [79]. For example, one can use genomic offset methods to identify loci important for local adaptation and predict the degree of **maladaptation** (offset) in future climates [80]. Adjusting fitness estimation approaches to environment-specific scenarios for different taxa can help identify adaptation costs in diverse ecological and evolutionary contexts.

Of the systems we have discussed, the ones that exhibit adaptation costs are often associated with specialized traits or trade-offs that occur under specific ecological scenarios, especially in rapidly fluctuating environments. As such, the trade-offs that are most relevant for supporting specialization and species coexistence in novel environments can also lead to limited or slowed evolution. We suggest that future experiments should focus efforts on species- or system-specific traits that are involved with adaptation. On the basis of our examples, these traits are likely to be the ones most associated with adaptation costs and can give a thorough appreciation for the consequences involved with global change (i.e., reduced rates or limited adaptation) and provide the most accurate estimates for population persistence. Empirical identification of these trade-offs can lead to predictions for rates of evolutionary rescue during global change because the fitness consequences of adaptation costs in variable or fluctuating environments are driven by these trade-offs.

Concluding remarks

Adaptation – whether in response to climate change, pesticides, biological invasions, or other anthropogenic selection pressures – can potentially rescue populations from demographic decline or extinction. However, the examples we have discussed here reveal some of the potential consequences that can accompany adaptation, ranging in type, severity, and ecological impact. As

Outstanding questions

How do adaptation costs scale with levels of population genetic variation, and to what extent could genomic variation predict whether trade-offs will arise?

Are adaptation costs more likely to occur under multiple stressors that interact in complex ways relative to additive interactions or single stressors?

Can symbioses or species interactions impact adaptation costs, and to what extent can these lead to or impede evolutionary rescue?

To model whether evolutionary rescue can restore population growth, we need concrete information on whether fitness trade-offs or costs scale linearly or nonlinearly as the extent of adaptation increases. Likewise, how do costs of adaptation scale with selection strength?

When do adaptation costs lead to extinction events? Might observing these fitness costs serve as indicators for species or populations that are more susceptible to extinction events?

environments continue to change rapidly and become more dynamic in the Anthropocene, trade-offs can lead to adaptation costs that limit fitness even when there is high standing genetic variation within populations. However, we have yet to fully account for these trade-offs in predictions of evolutionary rescue and still have much to understand about when they arise and how they may impact population resilience to anthropogenic change (see Outstanding questions). As global change accelerates, accounting for adaptation costs will enable ecologists, evolutionary biologists, and global change researchers to better predict and counter the effects of anthropogenic change in ecosystems.

Declaration of interests

The authors have no interests to declare.

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