Forum

Evolutionary theory as a tool for predicting extinction risk

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Timely and proactive wildlife conservation requires strategies for determining which species are most at the greatest threat of extinction. Here, we suggest that evolutionary theory, particularly the concept of specialization, can be a useful tool to inform such assessments and may greatly aid in our ability to predict the vulnerabilities of species to anthropogenic impacts.

Predicting the fate of species in a changing world

Species vary widely in how they are affected by environmental disturbance. Human-induced changes in the environment expose species to novel conditions that did not exist in their evolutionary past, and responses of species can impact their extinction risk [1]. Quantifying extinction risk is an important goal for conservation biologists and wildlife managers who must identify and prioritize species or populations. However, quantifying this risk is challenging, because populations can decline, stabilize, or even increase in the face of environmental change. Authors have discussed the importance of natural history and evolutionary information for assessing extinction risk [2,3]. These methods often require extensive life-history or detailed distributional data, which are optimized for *r*-selected terrestrial species (e.g., insects), but are less operational for larger and more-threatened *k*-selected consumers, especially those that are inherently rare, elusive, and difficult to study.

A framework for integrating evolutionary concepts (i.e., specialization) into risk assessment that can be applied to identify which ecological mechanisms expose various species to extinction risk is warranted. Much of the discussion on specialization has focused on extreme (generalist and specialist) individual species; however, specialization is a continuum, with most species falling between extremes. Thus, we lack a comparative methodological perspective of how the vulnerability of species can be compared along this quantitative axis for evolutionary traits and how these traits might be integrated into assessments of extinction risk.

Specialization as a tool for assessing ecological resistance

An important principle in evolution is that of specialization. As noted by others [4], ecologists have typically defined a specialist as a 'species that occupies a relatively narrow niche or restricted range of habitats, or alternatively a species or population that selects resources out of proportion to availability.' Specialization is a species-level phenomenon and can be measured in different ways (e.g., diet, temperature, morphology, etc.) and is tied to the concept of trade-offs [5]. The 'jack-of-all-trades-master-of-none' principle implies not only that lower levels of specialization (i.e., generalist) enable species to access a wide array of resource niches with relatively equal effectiveness, but also that there are limitations on the ability to efficiently access certain resources. Specialists should be able to access a single resource more effectively, at the expense of accessing a wider range of resources. This suggests that highly specialized species can be disproportionately vulnerable to human-induced environmental change. Conversely, highly generalized species are likely to be less vulnerable to such pressures. Furthermore, the correlation between phenotypic value and fitness of traits might change between environments, in which specialized traits can become maladaptive under altered selective pressures (Box 1). Recent work on sharks has shown that evolutionarily unique species are suffering declines and becoming increasingly extinction prone at faster rates than their more-generalized counterparts [6]. Here, we discuss three examples that demonstrate how viewing specialization as a continuum can inform our understanding of extinction risk (Figure 1).

Taxonomic case studies

Migratory Pacific salmon

Pacific salmon are notable for their remarkable long-distance migrations from freshwater habitats where they hatch (and return to reproduce) to ocean feeding grounds.

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Box 1. The continuum of specialization affects performance in changed habitats

As shown in Figure IA, specific traits of specialist species (designated S1 and S2) perform well under certain conditions or a smaller subset of resources (environment 1 and 2, respectively). A generalist species (G1) theoretically performs the same in both environments, but can also adapt to become increasingly fit when exposed to conditions that are unlikely to have existed in their evolutionary past (e.g., invasive species; G2). Tiger sharks are apex marine predators and the largest predatory fish in tropical waters worldwide, with recent research suggesting that they are functional, behavioral, and dietary generalists in almost all the ecosystems that they inhabit [6]. Tiger sharks have evolved specialized dentition (Figure IB,C) that has afforded them the ability to cut through the hard carapaces of sea turtles, a preferred prey species that shares a convergent distribution across subtropical and tropical marine habitats globally (Figure ID). Despite massive population declines in sea turtle species over the past century, particularly in the Atlantic Ocean, tiger sharks retain one of the most plastic and adaptive diets of all vertebrates, and their populations seem to be stabilizing or starting to increase despite persistent anthropogenic pressures that are causing other species to decline [6]. Thus, the lability of the cognitive and behavioral processes that dictate foraging and diet may offset the costs that might have been incurred from selective regimes favoring specialized teeth. This case study demonstrates the validity in using a multispecies, multifactor comparative framework for assessing and predicting extinction risk.

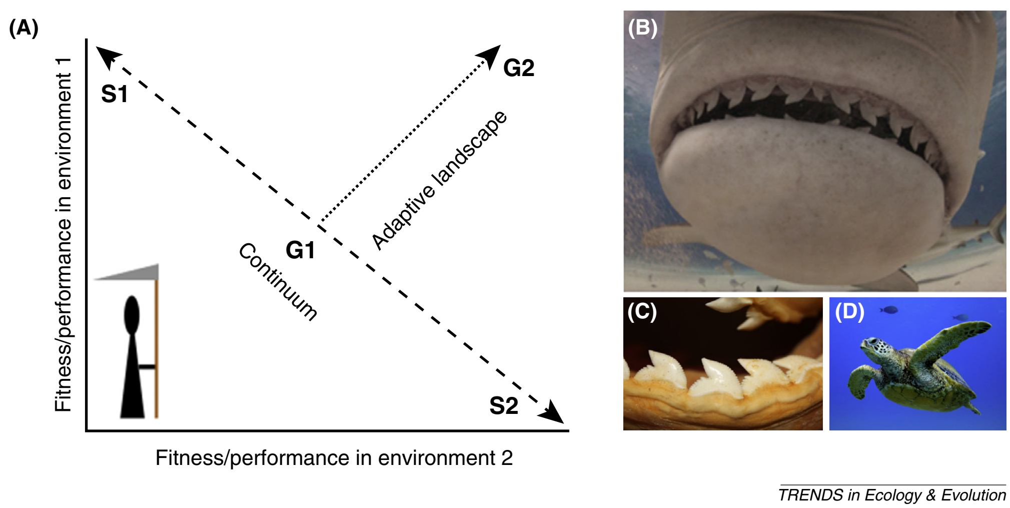

Figure I. The plasticity of ecological traits among threatened vertebrates. Photos B and D used, with permission, from Joe Romeiro and Orvil G. Clark (Oahu, HI, USA), respectively.

Salmon are sensitive to various human-induced environmental changes, including habitat alteration and climate change, and some Pacific salmon populations are critically endangered, while others are extinct [7]. The degree of habitat specialization seems to predict sensitivity to habitat degradation or loss, which can be independent of species range. Species that show extreme philopatry (e.g., sockeye salmon) can be more sensitive to habitat degradation on spawning grounds or rearing areas compared with allopatric species, such as pink salmon. Philopatric tendencies could limit straying when spawning habitats are degraded relative to allopatric species that have flexibility in spawning-ground selection. Physiological specialization is also important, as water and air temperature increase due to climate change. Those salmon populations that can maintain high-performance cardiovascular function at higher temperatures might be more resilient compared with populations that cannot [8]. This reveals the complex nature in which ecological or physiological specialization results in differential resilience to stressors.

Ectothermic lizards

One result of climate change is increases in temperature in different ecosystems, which are expected to increase extinction risk in ectotherms. Recent analyses indicate that global warming could disproportionally impact tropical ectotherms, because these species tend to be thermoconformers, whereas temperate ectotherms in temperate climates tend to be thermoregulators. Theoretical and empirical studies show how the degree of thermal specialization is closely tied both to ongoing population declines in reptiles and future extinction risk [9]. Lizard species that are thermoregulators can better cope with thermal stress compared with thermoconformers, which lack the behavioral capacities to adjust to alterations in temperature. Extreme thermal specialization often occurs in lizards that occupy stable thermal environments, such as montane cloud forests. For example, the Puerto Rican blue-chinned anole (*Anolis gundlachi*) is a thermoconformer that is confined to the cloud forests of El Yunque in Puerto Rico and, thus, faces higher risks from rising temperatures compared with its closely related congener, the crested anole (*Anolis cristatellus*), which is a thermoregulator that can occupy a wide range of thermal environments in and around El Yunque [9,10]. Accordingly, there is strong evidence that montane reptiles and amphibian populations are especially vulnerable to elevated global temperatures, whereas lowland populations are at lower risk [10].

Deep-diving pinnipeds

In marine mammals, successful foraging relies on the interaction between the physiology (i.e., ability to dive), behavior (i.e., how it dives), and the ecology (location and