Niche contractions in declining species: mechanisms and consequences

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Abstract

A fundamental aim of conservation biology is to understand how species respond to threatening processes, with much research effort focused on identifying threats and quantifying spatial and temporal patterns of species decline. Here, we argue that threats often reduce the realized niche breadth of declining species because environmental, biotic and evolutionary processes reduce or amplify threats, or because a species' capacity to tolerate threats varies across niche space. Our 'niche reduction hypothesis' provides a new lens for understanding why species decline in some locations and not others. This perspective can improve management of declining species by identifying where to focus resources and which interventions are most likely to be effective in a given environment.

Patterns of species decline

The earth is entering a sixth mass extinction event, with global change pushing thousands of species towards extinction [1, 2]. The importance of understanding processes of species' decline for responding to this extinction emergency has long been recognized [3-5]. However, research on species declines generally focuses on investigating patterns of decline in geographical distribution [6, 7] and numerical abundance, and identifying threats. This focus on decline in range and population size is understandable given these parameters are often straightforward to evaluate, and correlate with extinction risk [8]. Here, we argue that a complementary focus on reductions in the realized niche breadth of species will be, in many cases, more informative for understanding processes driving declines and developing conservation strategies than simply focusing on geographic patterns.

The niche reduction hypothesis

The niche concept provides a powerful approach to studying environmental and biotic factors that constrain species' distributions [9, 10]. We propose the 'niche reduction hypothesis', whereby heterogeneity in threat impacts across environmental space can result in reductions in the realized niche breadth of declining species (Figure 1). Acknowledging ongoing debate around niche terminology [11], we describe our niche reduction hypothesis in the context of Hutchinson's fundamental and realized niches, with some modifications to incorporate more recent conceptual developments (see Glossary) [10, 12].

Much research on species' declines implicitly assumes that the impact of threats such as climate change, land clearing, and introduced organisms is driven by the magnitude or abundance of the threat [13, 14]. However, a growing body of research has demonstrated that environmental conditions, biotic interactions, or disturbances can reduce or amplify the impacts of threats on aspects of a species' ecology, or the capacity of a species to persist in the presence of those impacts [15-18]. The resulting heterogeneity in threat impacts (and threat tolerance by species) across environmental space can drive changes in species' niche breadth. For example, threats such as non-random habitat loss [19] might eliminate species from lowland areas of their niche, while other threats such as exotic predators, might exclude species from parts of their niche where low habitat complexity amplifies predation rates [15]. The niche reduction hypothesis relates primarily to the realized niche, as a species' fundamental niche is genetically and physiologically determined and can be altered only by evolutionary processes [12, 20]. Importantly, the niche reduction hypothesis focuses on changes to niche breadth in multidimensional environmental space, rather than changes in the location or extent of a species' niche in geographic space (although changes in niche space and geographic space can be related).

The niche reduction hypothesis provides a new lens of analysis that focuses on contextualizing threats in terms of their impact on the realized niche breadth of species. This is important because when a species' contracts from its pre-threat realized niche (historical niche), to a narrower subset of environmental space (the contemporary niche), it can experience reduced ability to tolerate other threats, as well as lowered adaptive capacity and genetic diversity [10]. The niche reduction hypothesis brings together ecological and evolutionary processes that shape species declines and has the potential to provide new insights into the mechanisms driving species loss, and why species decline more severely or rapidly in some environments than others. Our approach emphasizes diagnosis of processes that determine threat impacts, and species' tolerance of threat impacts. This focus on processes can help determine what management approaches are appropriate and where to prioritize management actions. Here, we outline three broad categories of processes by which threat-driven niche reductions can occur.

Processes resulting in niche reduction

A. Heterogeneity in the occurrence or impacts of threats in environmental space

Environmental conditions can moderate the distribution of threats, or the severity of threat impacts, resulting in the contraction of a species' realized niche to a subset of the environmental conditions occurring in its historical niche. We identify three subtly different mechanisms by which this can occur: (i) environmental conditions limit threat distribution (threat absent); (ii) environmental conditions reduce or amplify the severity of threat impacts; and (iii) geographic barriers prevent threat occurrence in a subset of a species' range, potentially resulting in an incidental reduction in realized niche breadth. Below, we describe and illustrate each process with case studies.

Environmental conditions can limit threat distribution, resulting in contractions of species to areas where the threat is absent and a corresponding reduction in realized niche breadth (Environmental refugia, Figure 1A). For example, high elevation dry forests provide refuges for many declining, native Hawaiian birds from an introduced threat, avian malaria [21, 22]. Malaria causes severe mortality at low and intermediate elevations, which excludes many bird species from resource-rich, lowland, wet forest. The mosquito vector crucial for malaria transmission is currently absent at high elevations, allowing birds to persist [21, 23]. Another example is the widespread clearing of lowland vegetation for agriculture, causing species, such as the Bougainville monkey-faced bat (*Pteralopex anceps*) in Papua New Guinea, to be unable to occupy lowland rainforests (because they no longer exist) and resulting in a contraction of the species' realized niche to high elevation moss forests [24].

Environmental conditions can reduce or amplify the severity of threat impacts, allowing species to coexist with threats or excluding them from areas with high threat impact, respectively (Threat reduction and threat amplification, Figure 1A). When threat reduction or amplification occurs in only part of a species' realized niche, its niche breadth can be reduced. For example, the spread of introduced brook trout (*Salvelinus fontinalis*) has contributed to the decline of endangered bull trout (*Salvelinus confluentus*) through competition and hybridization [25]. However, while brook trout can occur throughout the bull trout niche, they have a higher thermal optimum than bull trout. Unfavourable thermal conditions for brook trout in high elevation headwater streams reduce their competitive advantage and the incidence of hybridization [25]. Thus, bull trout have contracted to high elevation areas where they are competitively superior.

Another example of threat reduction is reduced pathogen impacts in environments unfavourable for the pathogen. For instance, the emergence of chestnut blight (*Cryphonectria parasitica)* has resulted in the contraction of the American chestnut (*Castanea dentate*) to dry, high disturbance areas where disease impact is reduced. This represents a major reduction in the realized niche breadth of the American chestnut [26]. This example, and others (e.g. white nose syndrome in bats [27, 28]), highlight how the emergence of new biotic interactions can reshape the contemporary niche of impacted species; restricting them to areas where threat impact is environmentally reduced.

Interactions between several co-occurring threats, or threats and environmental conditions, can amplify the severity of threat impacts in certain parts of a species' realized niche, thus removing the corresponding set of environmental conditions from the contemporary niche.

There is growing recognition that complex interactions between anthropogenic disturbances and threatening processes drive species declines [15, 16, 29]. For example, the noisy miner (*Manorina melanocephala*), a native, disturbance-tolerant honeyeater, has increased in abundance in degraded woodlands in Australia, leading to frequent aggressive interactions with sympatric bird species that can result in local extirpation [30]. Importantly, in high quality woodland or areas with densely planted revegetation, noisy miners are less abundant, and have minimal impact on bird community structure [31, 32]. Thus, vulnerable bird species are excluded only from areas of their historical niche where they are subject to both habitat degradation and negative interactions with noisy miners, but are capable of persisting with each threat in isolation.

Finally, geographic refugia (Figure 1A) also can enable persistence of declining species in areas where threatening processes are absent. Geographic refugia can occur when barriers restrict threat distribution, resulting in incomplete overlap with the distributional extent of an impacted species. For example, nearshore islands often provide refuges for species extirpated from adjacent mainland regions by introduced predators [6], such as the contraction of little spotted kiwis (*Apteryx owenii*) in New Zealand to offshore islands where introduced mammalian predators are absent [33]. Although resulting from geographic, rather than environmental barriers, this can lead to an incidental reduction in niche breadth when only a proportion of the species' historical niche is represented in the refugia.

B. Heterogeneity in species' tolerance of threat impacts in environmental space

A species' capacity to tolerate a given magnitude of threat impact can vary across its niche space (in response to environmental conditions), driving a reduction in realized niche breadth. Here, we use the term ‘threat impact’ to describe the effects of a threat on the vital rates (e.g. mortality) of a species. Threat tolerance is the ability of a species to persist despite a given threat impact. For example, the capacity of Australian alpine tree frog (*Litoria verreauxii alpina*) populations to tolerate mortality associated with chytrid fungus (Box 1) is dependent on environmental conditions [34]. High disease impact in adults truncates age structure, resulting in the loss of long-lived adults capable of reproducing across multiple years. Prior to disease emergence, iteroparity buffered populations in ephemeral wetlands from periodic recruitment failure due to drought [34]. Reduced capacity to tolerate recruitment failure has resulted in this species contracting to drought-proof perennial wetlands; representing a major reduction in realized niche breadth [34].

More broadly, variation in individual or population growth rates in response to environmental conditions can determine whether threats cause population declines. For example, when environmental conditions are conducive to high adult survival or high reproductive rates, populations have a greater capacity to tolerate threat impacts. In contrast, populations exposed to threats in marginal environments can have limited capacity to tolerate threat impact [35]. For example, ectotherms occupying high elevation habitats are characterized by slower growth rates and longer times to reach reproductive maturity, compared to those living in lowlands [35]. High elevation populations are therefore less able to tolerate a given level of adult mortality compared to lower elevation populations, resulting in the same level of threat impact causing disproportionate declines in populations in high elevation habitats [36]. Variability in a species’ capacity to tolerate relatively uniform threat impacts can result in contraction of the contemporary realized niche to optimal habitat [6], with parts of the historical niche either unoccupied, or acting as ‘sinks’ for individuals dispersing from optimal habitat.

C. Evolutionary shifts

Emerging threats also have the potential to drive evolutionary changes in impacted species, affecting both realized and fundamental niches (Evolutionary shifts, Figure 1C) [20]. Evolutionary responses can allow species to re-expand into their historical niche, after an initial decline, when such responses either reduce the severity of threat impacts or increase the species' capacity to tolerate those impacts. For example, there is evidence that an evolutionary response in the bird, the Hawaii amakihi (*Hemignathus virens*), is facilitating re-expansion into low elevation parts of its historical niche where it experienced severe declines associated with the emergence of avian malaria [22, 23]. Similarly, evolutionary shifts, such as morphological adaptions to urban environments, can increase species' capacity to exploit novel environments [37], potentially facilitating an expansion in fundamental niche breadth.

Although the examples above demonstrate the capacity for evolutionary responses to partially overcome niche contractions, the processes by which threats reduce realized niche breadth also can reduce genetic diversity in declining species. This can potentially limit capacity for re-expansion or evolutionary responses. Local adaptation to environmental conditions has been demonstrated in a wide variety of species [38], and an increasing number of studies have documented associations between genetic diversity and local adaptation [39, 40]. Therefore, loss of realized niche breadth is likely to be associated with loss of adaptive genetic diversity [41]. This might constrain evolutionary responses to future environmental change and the capacity of a species to shift outside its contemporary niche [10]. This has practical relevance because conservation strategies that focus on evolutionary processes (e.g. climate-adjusted provenancing

[42] and other assisted migration strategies [43]) depend on the presence of environmentally-adaptive genetic diversity.

Applying the niche reduction hypothesis to improve conservation outcomes

In the following sections, we outline how recognizing changes in a species' realized niche can help parameterize the operating space for conservation actions. We highlight the differences between, and opportunities presented by, managing for conservation within the contemporary niche versus managing in the historical niche.

Recognizing reductions in realized niche breadth

An important first step in applying the niche reduction hypothesis to species conservation is recognizing that the potential operating space for conservation interventions can be much broader or narrower than the current understanding of a species' realized niche. For long-declined species, limited knowledge of the historical niche can lead to an overly narrow understanding of the species' potential or optimal niche space [44]. For example, the last known populations of the takahe (*Porphyrio hochstetteri*) occurred in sub-alpine grasslands, and this was assumed to represent preferred habitat for this bird in New Zealand [45]. However, subfossil and genetic evidence indicates that the species was historically widespread across a diverse range of lowland environments and subsequent introductions to lowland islands have been successful [46]. Without good historical knowledge, management actions can unnecessarily be restricted to the species' contemporary niche [44], where capacity for conservation gains might be more limited than in the historical niche (Figure 2). Conversely, for recently-declined species, estimates of habitat requirements and demographic parameters that were attained prior to decline can poorly reflect the current characteristics of the species (particularly if the niche contraction has resulted in a loss of genetic diversity). Finally, awareness of the potential for time-lagged extinction debts is important [47]. When extinction debts are in action, the current distribution of a declined species might be much broader than the contemporary niche (in which populations of the species are viable). For example, following a contraction in niche breadth, a long-lived plant species might survive, but no longer reproduce in a given portion of its historical niche [e.g. 48].

Conservation in the contemporary realized niche

Focusing conservation efforts in the contemporary niche of a declined species is important when strategies to reduce or eliminate threat impacts are not feasible in the historical niche. Conservation efforts in the contemporary niche are often focused on increasing the geographic extent of the contemporary niche (e.g. through translocation to unoccupied areas, or creation of new areas that correspond to the contemporary niche conditions). Efforts can also focus on identifying what characteristics of the contemporary niche allow species persistence and designing actions to maintain and improve them. For example, alpine tree frogs have been extirpated from ephemeral wetlands by disease and persist only in perennial wetlands [34]. As pathogen eradication or disease prevention in the historical niche is not feasible [49], a practical conservation option is to create additional perennial wetlands to increase the extent of the species’ contemporary niche.

While environmental reduction of threat impacts can underpin species persistence in the contemporary niche, it is important to recognize that threat reduction might occur in areas that are otherwise sub-optimal for the species. For example, areas with structurally complex vegetation that allow many small Australian mammal species to persist in the presence of introduced predators, have been perceived as preferred habitat for such species [44, 50]. However, these areas can lack important resources (e.g. preferred food), and encompass only a small proportion of the species historical niche space [29, 44, 50]. Thus, conservation efforts focused on trying to eliminate or reduce threat impact in such habitats might be ineffective because resources, rather than predation, might constrain population abundance. Instead, conservation efforts could focus on environmental management to increase resource availability within complex habitats, or increase habitat complexity in areas adjacent to where the species has persisted to allow re-expansion into more productive environments [15, 51, 52] (Figure 2).

Conservation in the historical niche

Many conservation actions fall into the category of management of the constraints on the contemporary niche (allowing reoccupation of the historical niche) by targeting the threat directly, or the environmental conditions or interactions underpinning the impact of the threat (sections A and B above). For example, in arid Australia, many native species are endangered by exotic cat and fox predation. Significant resources have been concentrated on predator control [53], with many local successes when used in conjunction predator exclosure fencing [54]. However, under certain conditions, a more effective way to mitigate this threat could be through control of invasive rabbits (*Oryctolagus cuniculus*); a species that inflates exotic predator abundance, and reduces vegetation cover, amplifying predation on native species [55]. Indeed, biological control of rabbits has been associated with reduced exotic predator abundance and subsequent recovery of endangered species [55].

Reintroductions and assisted colonization can be used to establish populations of a declining species in parts of its historical niche or unoccupied parts of its fundamental niche, respectively. However, reintroductions into the historical niche are likely to fail if the species has experienced a reduction in realized niche breadth, and the threat has not been mitigated. While direct threat mitigation is sometimes possible, in many cases, a complementary focus on identifying recipient sites where environmental conditions reduce threat impact, or managing sites to actively increase environmental threat reduction (e.g. re-creating important characteristics of the contemporary niche within the historical niche), might be more effective (Figure 2). When threat eradication or reduction is not possible, assisted colonization to unoccupied geographic refugia, such as offshore islands within the species fundamental niche, is an option [56]. When identifying recipient islands or locations for other intensive threat mitigation activities (e.g. predator-proof fencing), it is important to consider the species' fundamental niche requirements, rather than trying to match sites to those where the last remnant populations persist, which might poorly represent the historical niche breadth of the species.

Concluding remarks

Understanding how threatening processes impact declining species is a central focus of conservation biology. Similarly, the niche concept is an enduring paradigm in ecology. Yet integration of these two ideas in the context of declining species has received limited attention. We argue that species' declines are commonly associated with reductions in realized niche breadth. These niche contractions are underpinned by heterogeneity in the occurrence or impacts of threats, or variation in species' capacity to tolerate threat impacts across environmental space. In an era of mass biodiversity loss, understanding how threats shape the realized niche of declining species can assist the development of new management responses and identify where to prioritize conservation actions.

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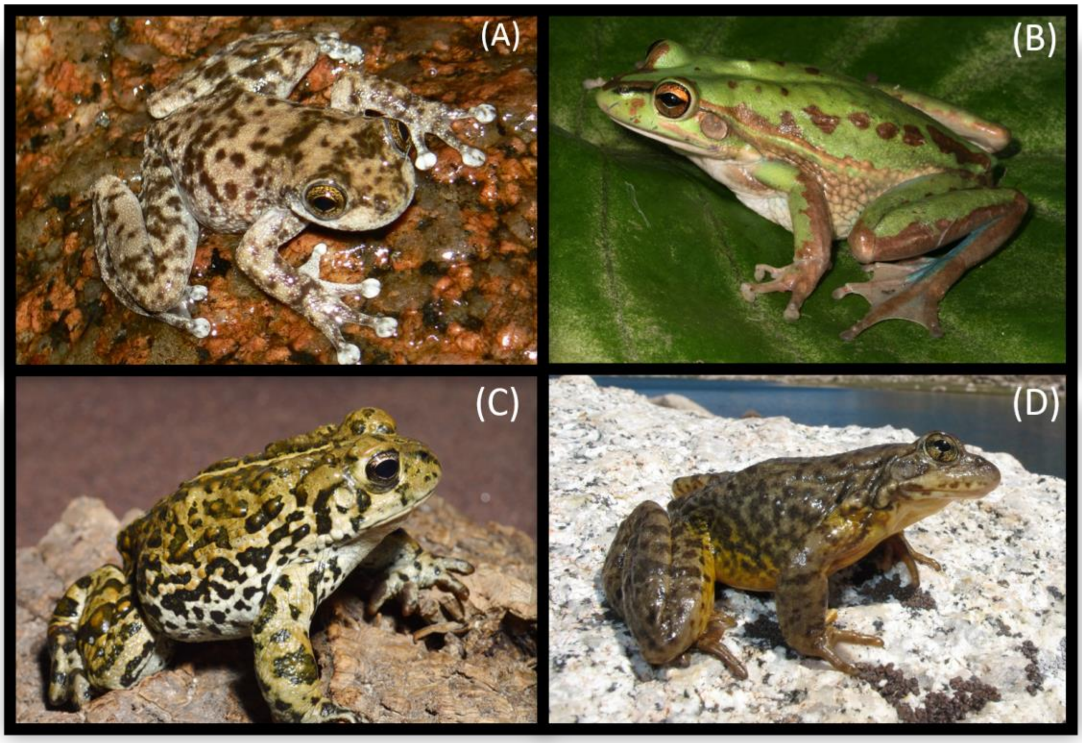
Box 1. Reduced niche breadth in amphibians impacted by disease.

The global emergence of chytrid fungus (*Batrachochytrium dendrobatidis*) – a pathogen that infects over 600 amphibian species worldwide – provides an example of the different processes by which a single threat can reduce the realized niche breadth of different species. **A. Heterogeneity in the occurrence or impacts of threats in environmental space:** Chytrid fungus growth is dependent on favourable environmental conditions; areas with sub-optimal temperatures and humidity provide refugia for frogs, where the pathogen is present, but infection intensity (and hence mortality) is reduced. Species such as the armoured mistfrog (*Litoria lorica*) (Figure I A), have been extirpated from closed canopy rainforest sites and now persist only in open savanna sites that are sub-optimal for the fungus [57]. Heterogeneity in threats in geographic space can also result in incidental reduction in niche breadth in environmental space, when species contract to areas (and the corresponding set of environmental conditions) where the threat is absent (Geographic refugia). Chytrid fungus remains absent from some islands adjacent to infected mainland regions. Isolated, uninfected islands can act as geographic refugia for amphibian species that are extinct or highly threatened on adjacent mainlands, such as the green and golden bell frog (*Litoria aurea*) (Figure I B) [58]. **B. Heterogeneity in species' tolerance of threat impacts in environmental space:** A species' capacity for demographic buffering of chytrid-induced mortality can be influenced by environmental conditions. For example, high recruitment in boreal toad (*Bufo boreas*) (Figure I C) populations at low elevations appears to offset adult mortality associated with chytrid, while populations at high elevations – on the edge of the species' environmental limits – have limited capacity for compensatory recruitment and are more vulnerable to decline [36]. **C. Evolutionary shifts:** Some species that were initially highly susceptible to chytrid fungus appear to be evolving resistance to the pathogen. An example is the endangered Sierra Nevada yellow legged frog (*Rana sierrae*) (Figure I D), which has experienced sustained recovery despite ongoing pathogen presence [59], potentially allowing the species to reoccupy parts of its niche after major declines. **Applying the niche reduction hypothesis to improve conservation outcomes:** Recognizing chytrid-associated reductions in realized niche breadth has been crucial to the development of innovative management solutions, including assisted colonization to environmental refugia within species fundamental, but not historically occupied niche, habitat manipulation to decrease environmental suitability for chytrid, and increasing population capacity for demographic buffering [49].



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Glossary

Contemporary niche: the realized niche occupied by a species following a reduction in niche breadth associated with threat impact.

Environmental refuge: a geographic location which corresponds to a set of environmental conditions where a threat cannot occur, and is within the fundamental niche of a declined species of interest.

Fundamental niche: the multidimensional environmental space under which a species could potentially persist and reproduce, in the absence of limiting biotic interactions and dispersal barriers. The fundamental niche is genetically and physiologically determined.

Geographic refuge: a geographic location where a threat is currently absent (e.g. due to dispersal barriers), but could potentially occur in the future, and that is within the fundamental niche of a declined species of interest.

Geographic distribution: the spatial extent of a species' distribution; analogous to area of occupancy.

Historical niche: the realized niche space occupied by a species prior to decline.

Niche breadth: the range of environmental conditions encompassed in a species' realized niche.

Niche reduction: a decrease in the realized niche breadth of a declining species associated with threat impact.

Range contraction: a spatial reduction in a species range. Commonly, but not always associated with a coincident reduction in realized niche breadth.

Realized niche: the multidimensional environmental space that a species occupies and maintains positive population growth. It is a product of a species' environmental tolerances, biotic interactions (both inter and intra-specific) and dispersal barriers. The realized niche can be spatially and temporally variable, and for some species, population growth can be dependent on the structure of this variability.

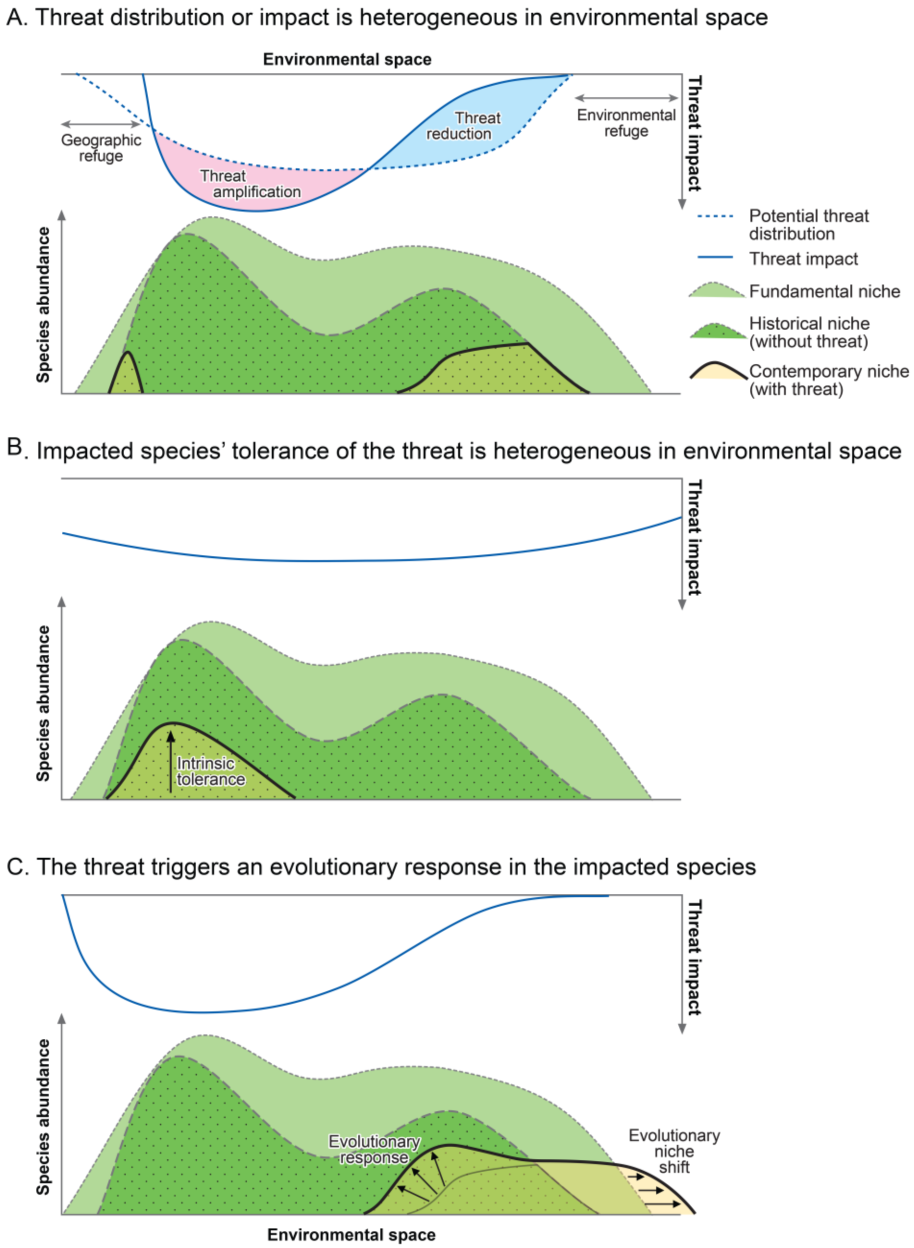
Reintroduction: the assisted establishment of a species within part of its historical niche where it has been extirpated.

Assisted colonization: the assisted establishment of a species within its fundamental niche, but outside its historical niche space.

Threat: a biotic or biophysical process that threatens the survival, abundance or evolutionary development of a species.

Threat impact: the effect of a threat on a certain aspect of a species' ecology. For example, reduced adult survival.

Threat tolerance: a species' capacity to persist given a certain level of threat impact. Capacity to tolerate threat impact can vary between populations of the same species depending on extrinsic and intrinsic factors of that portion of the niche. For example, differences in resource availability between populations can affect reproductive rates, and thus a population's capacity to tolerate a given level of adult mortality.



A. Threat distribution or impact is heterogeneous in environmental space

B. Impacted species' tolerance of the threat is heterogeneous in environmental space

C. The threat triggers an evolutionary response in the impacted species

Figure 1. Model of how environmentally heterogeneous threat impacts and heterogeneous responses of impacted species can alter realized niche breadth in declining species. Heterogeneity in species declines in environmental space can occur through three main mechanisms: (A) heterogeneity in the occurrence or impacts of threats in environmental space, which results in the impacted species contracting to parts of its niche where the threat is absent or has low-impact; (B) the impacted species' intrinsic capacity to tolerate threat impacts is

heterogeneous in environmental space, so the species contracts to parts of its niche with high intrinsic tolerance (e.g. high reproductive rate), and (C) after exposure to a threat, evolutionary responses in the impacted species might allow it to either re-occupy parts of its historical niche, or expand/shift its fundamental niche (and contemporary niche) into new environmental space. These processes can act individually, or in concert to generate differences between the historical and contemporary niches of a declining species, and this difference we refer to as reduced niche breadth.

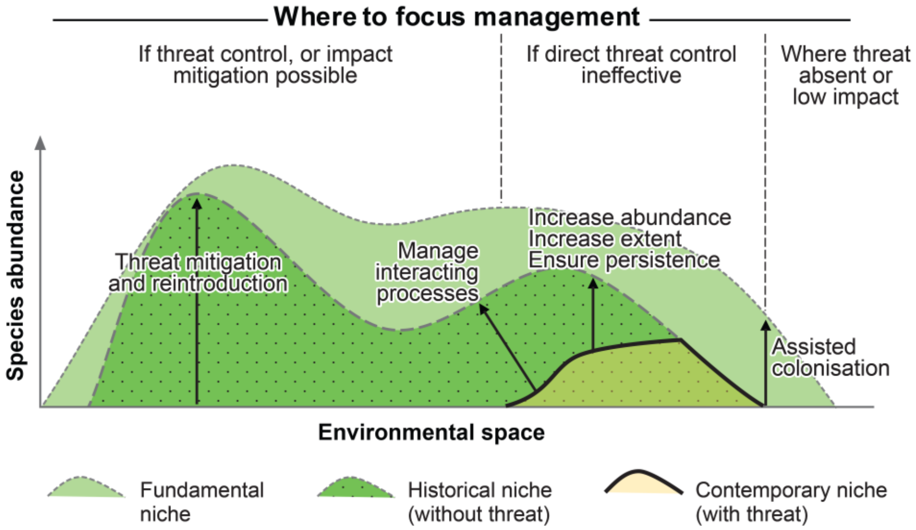


Figure 2. Using the niche reduction hypothesis to inform conservation actions. Where it is feasible to control or mitigate the impacts of a threat, then management within the historical niche, such as threat control and subsequent reintroduction, can have the greatest potential conservation gains. However, when threat control is not achievable, management within the contemporary niche to increase the abundance, expand the geographic extent (e.g. through habitat creation or translocation to environmentally similar but previously unoccupied areas) or improve the temporal stability of populations can be most beneficial. It might also be possible to work at the boundaries of the contemporary niche, using habitat manipulation, or managing interacting processes, to allow a species to re-expand into its historical niche. Finally, assisted colonization to create insurance populations in areas outside the realized niche (but within the fundamental niche), where the threat is absent or has low impact, might be useful to ensure the survival of highly threatened species.