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Title: The role of biotic interactions in the niche reduction hypothesis

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Main text:

The 'niche reduction hypothesis' (NRH) [1] postulates that declining species can experience reductions in their realized niche breadth because environmental, biotic, and evolutionary processes reduce or amplify threats, or because a species' capacity to tolerate threats varies across niche space. Doherty and Driscoll [2] embrace the NRH and then expand on one of the important biotic processes, interspecific competition, and its role both in contributing to contractions of species' realized niches, and as a potential barrier to niche re-occupation. Interspecific competition is indeed important in some species declines. However, competition is but one of many types of species interactions incorporated in the NRH under the umbrella term 'biotic interactions', which need to be considered when managing declined species (see 'Manage interacting processes' Figure 2 [1]).

A central theme of the scenarios highlighted by Doherty and Driscoll is that the threat-driven absence of a species from its historical niche can create a secondary threat to the recovery of the declined species if a competing species expands into the vacated niche space. Doherty and Driscoll pay particular attention to scenarios where the target conservation species is an inferior competitor, or has very specific habitat requirements. However, irrespective of any competitive dominance or inferiority, established populations can be difficult to dislodge from occupied niche space, both due to high levels of interspecific competition, as well as broader hysteresis effects which might occur within ecosystems. Indeed, the role of historical contingencies in structuring ecological and genetic patterns (priority effects or density blocking) is well recognised in community ecology and biogeography [3, 4].

From a conservation perspective, the niche that a species is able to reoccupy after a decline might be narrower than its historical niche. Doherty and Driscoll give an example of the red wolf (*Canis rufus*), which before its decline, was a dominant competitor over coyotes (*C. latrans*). They suggest that now coyotes are abundant in areas where red wolves have been extirpated, resource competition might restrict the re-establishment of the red wolf. However, red wolf recovery is also inhibited by ongoing human persecution, as well as hybridization with coyotes [5]. In addition, extensive habitat modification [5] could mean that the remaining available habitat is outside the optimal niche of wolves, and favours the coyote which can exploit disturbed environments. Therefore, while competition with coyotes could be one factor preventing wolves from reoccupying their historical niche, other biotic interactions, as well as changes in the geographic extent of the wolf's optimal habitat, are also likely to be important factors. It is important to distinguish between niche space, and the geographic availability of that niche space, when applying niche theory to conservation.

When species experience major declines, simply removing the primary threat(s) that drove the decline can fail to facilitate species recovery. Biotic interactions, including intraspecific interactions, predator-prey interactions, and commensal, facilitative, parasitic and mutualistic relationships, can determine whether a declined species can re-occupy its historical niche. Altered biotic interactions might become particularly important when primary threats and species declines have been occurring for many years and ecosystem and community dynamics have shifted. For example, successful restoration of plant communities can be dependent on the re-establishment of facilitative soil biota [6]. Similarly, the recovery of the large blue butterfly (*Maculinea arion*) in England was dependent on re-establishing suitable habitat conditions for the red ant (*Myrmica sabuleti*), a species on which the large blue butterfly caterpillar has a parasitic dependency [7]. These examples, and the interspecific competition processes raised by Doherty and Driscoll, highlight the crucial role of biotic interactions in species recovery efforts.

Too often, conservation efforts are focused on the abiotic requirements of species for persistence, and the complexities of the multiple interacting processes shaping species occurrence and responses to threats are under-appreciated. The NRH provides a framework to consider species declines and conservation management in terms of the biotic and abiotic processes influencing the realized niche of declined species. The NRH aims to improve opportunities for drawing on ecological theory for applied conservation research and management. In the face of the emerging extinction crisis, the NRH can facilitate new insights into the causes of species decline, barriers to recovery, and options for innovative management solutions.

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