

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

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9 **Keywords:** biotic interactions, endangered species, niche theory, species recovery

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11 **Main text:**

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

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

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

45 When species experience major declines, simply removing the primary threat(s) that drove
46 the decline can fail to facilitate species recovery. Biotic interactions, including intraspecific

47 interactions, predator-prey interactions, and commensal, facilitative, parasitic and mutualistic
48 relationships, can determine whether a declined species can re-occupy its historical niche.
49 Altered biotic interactions might become particularly important when primary threats and
50 species declines have been occurring for many years and ecosystem and community
51 dynamics have shifted. For example, successful restoration of plant communities can be
52 dependent on the re-establishment of facilitative soil biota [6]. Similarly, the recovery of the
53 large blue butterfly (*Maculinea arion*) in England was dependent on re-establishing suitable
54 habitat conditions for the red ant (*Myrmica sabuleti*), a species on which the large blue
55 butterfly caterpillar has a parasitic dependency [7]. These examples, and the interspecific
56 competition processes raised by Doherty and Driscoll, highlight the crucial role of biotic
57 interactions in species recovery efforts.

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

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