Letter

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A downside of diversity? A response to Gallagher *et al.*

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Niche theory as a predictor of extinction probability

Gallagher *et al*. [1] propose that the niche breadth of a species is a potentially reliable predictor of extinction vulnerability. Species with narrow niches (specialists) generally have lower ecological resistances (i.e., are more sensitive to environmental disturbances) than similar species with broader niches (generalists). Gallagher *et al*. demonstrate this relationship between niche breadth and extinction vulnerability by highlighting the elevated extinction probabilities for specialist versus generalist species across a broad range of taxonomic groups. We suggest that the incorporation of 'niche packing' theory allows us to predict which communities should have constituent species at greatest risk of extinction.

Specialists can be highly prone to local extinction following habitat loss because the resource(s) required by the species are often missing from any remaining habitats [2]. In the case of climate change, changes in temperature and precipitation regimes can quickly shift habitat conditions beyond the narrow requirements of specialized species [3]. Therefore, in the absence of rapid adaptation and 'evolutionary rescue', relatively minor changes in climate can force specialized species to shift their geographic distributions [4]. Even with migrations, specialized species will be at an inherent disadvantage because areas that offer both suitable climates and the required environmental conditions will be relatively sparse. By contrast, generalists will be better able to tolerate environmental changes because these species are by definition capable of persisting across a wider range of conditions.

Considering the strong connection between the degree of specialization of a species and its sensitivity to disturbance, we argue that extinction probability must then be predicted to be highest in those areas that support the largest numbers or proportions of narrow-niched species. Theory provides us with one tool for predicting where these specialist species are most likely to occur. Specifically, the theory of 'niche packing' states that, because of heightened interspecific competition, the species that occur in biologically-diverse communities will tend to have narrower niches (i.e., will be more specialized) than will similar species in less-diverse communities [5].

Taken together, these two theories – the increased sensitivity of specialized species and greater niche-packing in more diverse communities – dictate that the intrinsic extinction vulnerabilities of species should generally increase with diversity. In other words, we hypothesize that there is likely to be a 'downside to diversity', such that the species comprising more-diverse communities are inherently at greater risk of extinction than are species of depauperate communities.

The downside of diversity: a tropical problem?

The most biodiverse communities in the world are located in the tropics [6]. Tropical species are widely believed to be more sensitive to climate change than their temperate counterparts because of (i) the absence of a marked latitudinal gradient of temperature within the tropics, which results in greater distances between current and future climate analogs, and hence faster climate-change velocities, necessitating faster rates of species migration [7,8]; (ii) rapid rates of habitat loss which decrease habitat availability and increase the distances that species will be required to migrate to keep pace with changing climates [9]; and (iii) the prevalence of species with narrow climatic niches due to the short- and long-term climatic stability of tropical environments [10]. As discussed above, the diverse communities of the tropics will also generally exhibit intense interspecific competition and niche packing. Therefore, tropical species can be predicted to have narrower niches, even regarding non-climatic factors such as diet preference and habitat use, than their temperate counterparts [11]. According to our proposed 'downside of diversity' hypothesis, extinction probabilities may therefore be even higher in the biologically-diverse communities of the tropics than was previously anticipated.

With the massive number of extinctions that are forecast as we enter the 'Anthropocene' [12], it is crucial that we identify the systems and communities under greatest risk of species loss – we cannot afford to wait to construct models *post hoc* based on observed extinctions. Combining the theories synthesized by Gallagher *et al*. with the classic theory of niche packing, we can predict that highly-speciose communities and their constituent species are at high risk of extinction from environmental disturbances such as climate change and habitat loss. Given this potential downside to diversity, we argue that there is additional motivation to prioritize the conservation of high-diversity communities in the tropics.

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