

## One size does not always fit all: a reply to Stroud and Feeley

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In their response to our recent article on using evolutionary theory to predict extinction risk [1], Stroud and Feeley [2] suggest that extinction probabilities are highest in regions where there is a higher density of narrow-niched species. More specifically, Stroud and Feeley [2] suggest that incorporating theory of 'niche-packing' in our framework [1] might also be useful for predicting where extinctions may occur, due to the fact that competition between species will result in higher degrees of specialization. We commend Stroud and Feely [2] for highlighting these issues, but the framework we presented in [1] already integrated the theory of niche packing as it relates to extinction risk, although the term 'niche packing' was not explicitly used. In fact, in our framework, we included geographic range and population density, the two main points of Stroud and Feeley [2], as two of several parameters for estimating resilience.

There are also a few important assumptions provided in the discourse by Stroud and Feely [2] that we feel should be addressed. We are in agreement that the number of specialists inhabiting a specific area may indeed be frequency dependent due to competition and niche packing. However, stating that niche packing can generally predict extinction is not well supported currently, because the manner in which specialization acts on extinction risk is not necessarily a frequency-dependent process [3]. For example, Smith et al. [4] found that disease-mediated extinctions in amphibians in Central America created a homogenizing effect on the remaining species, thus rendering them increasingly 'generalist'. In addition, working across a latitudinal gradient in Central America, Lips et al. [5] found that the degree of decline of amphibian species did not differ among sites (i.e., different communities), but instead found that specific ecological traits (aquatic affinity, elevational specialization, and body size) were strong predictors of decline. Additionally, certain traits may weigh different-

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ly in how they contribute to the overall extinction risk of a species and, as we mentioned in our original paper [1], researchers are tasked at elucidating these patterns. Modeling approaches would be valuable for testing these assumptions.

In their response [2], Stroud and Feely also contend that 'species comprising more diverse communities are inherently at a greater risk of extinction than are species of depauperate communities', and point to the tropics as an example. While one might assume a higher level of extinction risk in tropical areas [6], this statement is suggestive that biodiversity itself promotes extinction. In fact, a large body of research shows that community diversity drives ecosystem stability to environmental disturbance [7,8]. Indeed, maintenance of biodiversity is a goal of conservation biologists, not only to limit extinction, but also to promote community resilience to human threats [7,8]. Moreover, the same argument could be made for temperate regions with lower diversity of species, where communities in these areas may retain a smaller overall 'trait space'. A disturbance of this community could have a similar (or even greater) net effect on vulnerability or extinction as one comprising many specialists in the tropics. The difficulty in validating these hypothetical scenarios is consistent with the goal of our original article of pointing out opportunities for theoreticians and modelers to use a framework and test these ideas.

Discussions made by both papers [1,2] on the utility of evolutionary and ecological theory to predict extinction risk also assume that specialists retain lower genetic variation in traits that are under selection in altered habitats. Data on specific traits for ascertaining thermal tolerance, for example, are likely to be lacking for large vertebrates. However, work on *Drosophila* spp. has shown that traits important for driving thermal tolerance have relatively high phylogenetic inertia, suggesting that adaptive distributional responses to climate change are limited [9]. The discovery of evolutionary traps in many larger vertebrate species can help identify where these types of ecological 'deadends' might lie, and could be used to launch investigations into the role of specialization on extinction risk [10].

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We are grateful for the productive discussions that our paper has already generated. We believe that the ideas added by Stroud and Feely [2] validate and help highlight the concepts espoused in our initial paper and those elsewhere [11]. We hope that such discourse will continue to generate new questions, focused investigations, and empirical data using our flexible framework that ultimately fosters the conservation of threatened species.

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