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.

References

1 Gallagher, A.J. *et al.* (2015) Evolutionary theory as a tool for predicting extinction risk. *Trends Ecol. Evol.* 30, 61–65
2 Diamond, J.M. *et al.* (1987) Bird survival in an isolated Javan woodland: island or mirror? *Conserv. Biol.* 1, 132–142
3 Schwartz, M.W. *et al.* (2006) Predicting extinctions as a result of climate change. *Ecology* 87, 1611–1615
4 Bell, G. and Gonzalez, A. (2009) Evolutionary rescue can prevent extinction following environmental change. *Ecol. Lett.* 12, 942–948
5 Case, T.J. (1981) Niche packing and coevolution in competition communities. *Proc. Natl. Acad. Sci. U.S.A.* 78, 5021–5025
6 Brown, J.H. (2014) Why are there so many species in the tropics? *J. Biogeogr.* 41, 8–22
7 Loarie, S.R. *et al.* (2009) The velocity of climate change. *Nature* 462, 1052–1055
8 Wright, S.J. *et al.* (2009) The future of tropical species on a warmer planet. *Conserv. Biol.* 23, 1418–1426
9 Feeley, K.J. and Rehm, E.M. (2012) Amazon's vulnerability to climate change heightened by deforestation and man-made dispersal barriers. *Global Change Biol.* 18, 3606–3614
10 Tewksbury, J.J. *et al.* (2008) Putting the heat on tropical animals. *Science* 320, 1296–1297
11 Belmaker, J. *et al.* (2012) Global patterns of specialization and coexistence in bird assemblages. *J. Biogeogr.* 39, 193–203
12 Corlett, R.T. (2015) The Anthropocene concept in ecology and conservation. *Trends Ecol. Evol.* 30, 36–41

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

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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 differently 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 'dead-ends' might lie, and could be used to launch investigations into the role of specialization on extinction risk [10].

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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References

1 Gallagher, A.J. *et al.* (2015) Evolutionary theory as a tool for predicting extinction risk. *Trends Ecol. Evol.* 30, 61–65
2 Stroud, J.T. and Feeley, K.J. (2015) A downside of diversity? A comment on Gallagher *et al*. *Trends Ecol. Evol.* 30, 296–297
3 Irschick, D.J. *et al.* (2005) Phylogenetic methodologies for studying specialization. *Oikos* 110, 404–408
4 Smith, K.G. *et al.* (2009) Selecting for extinction: nonrandom disease-associated extinction homogenizes amphibian biotas. *Ecol. Lett.* 12, 1069–1078
5 Lips, K.R. *et al.* (2003) Ecological traits predicting amphibian population declines in Central America. *Conserv. Biol.* 17, 1078–1088
6 Laurance, W.F. *et al.* (2012) Averting biodiversity collapse in tropical forest protected areas. *Nature* 489, 290–294
7 Cardinale, B.J. *et al.* (2012) Biodiversity loss and its impact on humanity. *Nature* 486, 59–67
8 Hooper, D.U. *et al.* (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486, 105–108
9 Kellerman, V. *et al.* (2012) Phylogenetic constraints in key functional traits behind species' climate niches: pattern of desiccation and cold resistance across 95 *Drosophila* species. *Evolution* 66, 3377–3389
10 Robertson, B.A. *et al.* (2013) Ecological novelty and the emergence of evolutionary traps. *Trends Ecol. Evol.* 28, 552–560
11 Hendry, A.P. *et al.* (2011) Evolutionary principles and their practical application. *Evol. Appl.* 4, 159–183