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Digest: Ecological opportunity, competition, and diversity dependence in macroevolution*

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The realization that adaptation can happen over observable time has accelerated our understanding of how competition can drive evolution. However, the extent to which competition influences macroevolutionary patterns remains a contentious issue. Classically, the relationship between competition and biodiversity dynamics was examined through the fossil record. More recently, reconstructed molecular phylogenies have provided an additional tool for modeling how species interactions may influence rates of species diversification and trait evolution. However, disentangling the processes of speciation from extinction using only information on extant lineages remains a major challenge (Marshall 2017). Progress in understanding the factors that influence rates of speciation and extinction is therefore integral to our understanding of how biological diversity is distributed and maintained at both regional and global scales (Rosenzweig 1995).

Early in their existence, clades often undergo an initial burst of diversification. One explanation for this pattern is the hypothesis of "ecological opportunity," where a species or clade presented with access to unexploited ecological resources rapidly expands in species abundance and ecological diversity (Schluter 2000). For example, colonization of the remote Hawaiian archipelago led to repeated diversification across a suite of plant and animal taxa, just as the colonization of landlocked African Rift Lakes was followed by the explosive diversification of freshwater cichlid fishes (Stroud and Losos 2016).

After this initial burst of diversification, whether early in a clade's existence or after encountering an ecological opportunity, speciation rates often tend to decrease as the number of taxa within a clade increases, a concept known as diversity-dependent diversification (Rabosky 2013). Diversity dependence is commonly interpreted as evidence for the effects of interspecific competition between taxa within a diversifying clade, but competition may also affect the macroevolutionary landscape between members of different clades.

In this issue, Pires et al. (2017) provide new evidence for both within- and between-clade diversity dependence influencing macroevolutionary patterns of speciation and extinction of terrestrial mammalian carnivores in North America and Eurasia. Using the fossil record to independently assess respective diversification dynamics, the authors found that increases in diversity were associated with decreased speciation rates in Eurasia and increased extinction rates in North America.

Following the invasion of Eurasia, North American carnivores encountered a wealth of unexploited ecological space, because there existed few species ecologically similar to themselves. The invading clades underwent rapid and spectacular evolutionary radiations, resulting in new Eurasian species of large-bodied bears (Ursidae), foxes and wolves (Canidae), and a suite of ecologically diverse weasels, otters, and badgers (Mustelidae). However, as more species accumulated, the rates of speciation within each clade slowed, providing support for diversity dependence of speciation rates within clades.

In North America, however, most clades did not show evidence for declining speciation rates as within-clade diversity increased. One possible explanation for this difference is that the presence and early radiation of Canidae in North America may have limited diversification opportunities for other clades, therefore lowering the importance of within-clade diversity dependence. In other words, the presence of an incumbent

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clade, such as the canids, may prevent (or limit) later clades from diversifying into ecologically similar forms (Rosenzweig and McCord 1991)—an evolutionary analogue of the ecological "priority effect" (MacArthur 1972). Instead, diversity dependence between clades had a stronger effect on extinction rates than speciation rates. In particular, the arrival and diversification of felids (cats and related species; Felidae) coincided with a decline in the diversification of canids in North America. Pires et al. (2017) argue that this provides evidence for between-clade diversity dependence mainly affecting extinction regimes.

Biologists will likely continue to debate the importance of diversity dependence and ecological limits to diversity (or, indeed, whether diversity is ecologically limited at all; Harmon and Harrison 2015). Pires et al. (2017), however, present an intriguing view of how the simultaneous processes of between- and within-clade diversity dependence may guide the dynamics of species diversification across entire continents and adaptive zones. Further studies at large phylogenetic scales, such as in their paper, will continue to broaden and develop the theory of diversity dependence on macroevolutionary patterns.

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