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update

Shadows of the past: paleo-reconstructions, phylogenies, and macroecological hypotheses

Macroecology has come a long way in providing a synthetic framework mainly by linking ecology and biogeography. Nevertheless, it has expanded its focus thanks to studies considering large temporal scales or which include species evolutionary information. Additionally, data are now available to reconstruct the climatic conditions and habitats at different locations in the past. This deep-time perspective allows more comprehensive analyses and fosters the integration of different approaches within the common framework provided by macroecology (Beck et al. 2012).

A recent study by Kissling et al. (2012) represents a good example of this trend and its implications for a comprehensive understanding of biodiversity patterns. Kissling and colleagues took advantage of the existence of a palm genera supertree and applied community phylogenetic, macroecological, and paleogeographic methods to understand the causes of current phylogenetic structure in palm species assemblages.

Linking specific historical processes to particular outcomes in assemblages' properties is not

an easy task. Kissling et al. (2012) exemplify how framing specific hypotheses can help in this endeavor (Table 1). They explicitly evaluated the effect of past events—such as habitat availability and biome loss over the Cenozoic—and climate change during the Quaternary on the phylogenetic structure of palm assemblages at different spatial scales (global, hemispheric, and biogeographic realms). By evaluating different spatial scales, they were able to infer which process acted at each scale and compare them among geographic regions of the world. Their results support an effect of *in situ* diversification and geographic isolation producing phylogenetic clustering, but not supporting the idea that time-integrated-area is a strong predictor of phylogenetic structure. Nevertheless, there were differences among biogeographic realms related to tropical forest loss during the Cenozoic. Furthermore, Quaternary climate change was responsible for phylogenetic clustering in South America and Africa. Interestingly, Kissling et al. (2012) found phylogenetic overdispersion at transitional areas where biotas

Hypotheses	Predictions	Results
H1: Geographic isolation has caused dispersal limitation and <i>in situ</i> diversification	Phylogenetic clustering within regions increases with an increasing spatial scale of the sampling pool	Agreement with H1: Higher phylogenetic clustering with increasing sampling pool (e.g., South America, Indomalaya, Australasia)
H2: Large areas over deep geological time have greater diversification rates ("time-integrated species-area effect" of Fine and Ree 2006)	Higher phylogenetic clustering in areas stable over deep geological time	Disagreement with H2: Phylogenetic clustering does not increase in stable areas (e.g., Africa)
H3: Cenozoic biome losses decreases diversification rates (higher extinction rates, less speciation)	Lower phylogenetic clustering in regions suffering greater biome loss	Agreement with H3: Random phylogenetic clustering in areas with greater Cenozoic biome loss (e.g., Africa)
H4: Quaternary climate change filters species able to survive and/or recolonize	Phylogenetic clustering increases in paleoclimatically low-stable regions	Agreement with H4: Higher phylogenetic clustering within Quaternary unstable areas (e.g., South America)

Table 1. A summary of the hypotheses, predictions and main results in Kissling et al. (2012).

interchange, suggesting an alternative application of NRI (Net Relatedness Index; Webb et al. 2002) to identify such areas.

The integration by Kissling et al. (2012) of geological, geographic, and paleoclimatic information along with phylogenetic information and current distribution of species certainly provides novel insights into the determinants of tropical biodiversity. Such a framework can be extended to other taxonomic groups (e.g., mammals), given the increasing availability of data at large spatio-temporal scales and supertrees. Although numerous drawbacks still need to be overcome, integrative studies such as this may pave the way towards the ultimate goal of understanding the underlying causes of biodiversity patterns. Macroecology has been fundamental in achieving this goal, providing conceptual bridges among different approaches from phylogeography to population and community ecology, to paleontology and macroevolution. Nevertheless, studies testing specific hypotheses with clear *a priori* expectations—which is the case of Kissling et al. (2012)—are fundamental to cross and, eventually, (re)build these bridges.

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