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Frontiers of Biogeography

Title

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Permalink

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Journal

Frontiers of Biogeography, 5(2)

Author

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Publication Date

2013

DOI

10.21425/F5FBG15938

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commentary

Getting a grip on global vertebrate biodiversity patterns?

Understanding what causes the global distribution of biodiversity is central to biogeography and macroecology. However, the mechanisms driving major patterns such as the latitudinal diversity gradient (“ecology’s oldest pattern”; Hawkins 2001) remain a scientific enigma. On the one hand, there are many plausible hypotheses that often lack consistently strong empirical support (Willig et al. 2003); on the other hand, we can make good spatial predictions of diversity from some simple environmental correlations without really understanding their causalities. Over the last decade great advances in data availability (regarding biodiversity and environmental factors) and spatial modelling have been made, and they are increasingly used to get closer to the root of the patterns (Beck et al. 2012).

Two recently published studies (Jetz and Fine 2012, Rosenzweig et al. 2012) addressed global species richness patterns in relation to environmental conditions. These studies not only used the same database of terrestrial vertebrate distributions (WWF¹), but they share several other conceptual and methodological aspects, as discussed below. Both studies accounted for a large portion of the between-bioregion (Jetz and Fine) or between-realm (Rosenzweig et al.) global variability in species richness ($R^2 = 0.78$ and $R^2 = 0.97$, respectively) from relatively ‘simple’ environmental models (i.e., few predictors). While such models have been presented before for a number of datasets, I liked the way they attempted to focus on predictors that are directly linked to theoretical concepts of underlying causality. Integrating ideas on ecological and macroevolutionary processes to understand biodiversity across spatial scales is increasingly the focus of macroecological investigations, with other approaches ranging from analysing experimental data over large extents to process- or individual-based, phylogenetically explicit simulation models (see Beck et al. 2012 for review).

In particular, there is broad agreement that macroevolutionary events such as speciation and extinction are the primary determinants of large-scale species richness patterns. However, most analyses have addressed species richness patterns based on grid cells much smaller than most species’ ranges, leading to a subtle overrepresentation of data for wide-ranging taxa (i.e., pseudoreplication). Both studies approached this problem by aggregating data into 32 ‘bioregions’ (Jetz and Fine 2012) or nine zoogeographic regions (Rosenzweig et al. 2012), that represent the ‘evolutionary arenas’ of relatively unique species communities (Jetz and Fine 2012), in which speciation and extinction have been played out.

Furthermore, both studies modelled environmental effects that can be linked to (hypothetical) causes of variation in speciation or extinction rates. Beyond considering temperature, area and productivity, Jetz and Fine (2012) followed Fine and Ree (2006) in time-integrating key variables, thus attempting to account for the fact that conditions have shaped the course of evolution (and hence current biodiversity) over time. Specifically, Jetz and Fine (2012) included productivity–area composites of biomes integrated over the last 55 million years, based on palaeoclimatic reconstructions, as predictors of current species richness. These capture the fact some biomes existed over large areas for a long time, whereas others only recently expanded in area. They also added, in a hierarchical manner, a finer-grained analysis to investigate how regional richness and productivity affected species sorting within bioregions. Even if it may be too early to judge the precision and reliability of area and productivity estimates across such long time scales, I think the aims (and success) of their approach need to be appreciated. Challenges remaining include incorporating montane regions (which Jetz and Fine 2012 excluded), investigating the actual strength of (regional) productivity effects and testing alternative hypotheses to those investigated by Jetz

¹ <http://worldwildlife.org/pages/wildfinder>

and Fine (2012).

Rosenzweig et al. (2012) concentrated on coarser-scale species richness patterns (i.e., species richness of zoogeographic regions) as a function of area and productivity (or temperature). They avoided using co-linear productivity and temperature within the same model to prevent potential misinterpretation of modelled effects, but this also precluded accounting for the separate effects that these variables could have on extinction and speciation. The authors used their well-fitting model to make far-reaching predictions on future human-caused extinction rates under different magnitudes of human appropriation of both area and primary productivity (calling it an “evolutionary telescope”). They concluded that there may be more severe forthcoming extinction effects than earlier studies had estimated.

These two studies, and their comparison, connect with other important frontiers in biogeographic research. (1) Rosenzweig et al.’s (2012) “telescope view” into the future ties in with the recent debate on the predictability of extinction rates from area loss (Beck 2011, Storch et al. 2012). (2) Rosenzweig et al. (2012) argue that Jetz and Fine’s (2012) integration of time and area to account for species richness inherently departs from the idea that regions attain a steady-state species richness (i.e., an equilibrium of speciation and extinction), but rather assumes continuous change of biodiversity with time. (3) Finally, both studies rely on defining regions of unique evolutionary history—one of biogeography’s oldest patterns (i.e., Wallace 1876), yet still an active field of research (Kreft and Jetz 2012, Holt et al. 2013).

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Edited by Michelle Greve and Richard Field