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Letter

# Diversity patterns are parsimoniously explained by equilibrium dynamics

David Storch [1,2,*], Grace I. Ridder [1,2], and Jordan G. Okie [3]

In our opinion article [1], we argued that addressing potential biodiversity equilibria is important even if diversity is often out of equilibrium, since the out-of-equilibrium state cannot be recognized without accounting for potential equilibria, and such a state is crucial for inferences associated with extinction and speciation debts and credits. Since nonequilibrium (historical) explanations of many biodiversity patterns, such as the latitudinal diversity gradient, are not more parsimonious or falsifiable than equilibrium explanations, neither of them should be considered the interpretive default.

We agree with Pie [2] that patterns in phylogenetic trees often appear compatible with nonequilibrium views. However, we argued that the nonequilibrium inference is often based on misleading interpretations of respective measures of extant phylogenetic trees (Box 1 of [1]) and improper theoretical framings for associated hypothesis testing. Unfortunately, this problem also includes the cited study by Pie *et al*. [5]. In that study, the authors found that clade density was not consistently negatively correlated with speciation rate, which they interpreted as a lack of evidence for a negative diversity-dependence of speciation rate. The problem is that both clade density and speciation rates were calculated using the same phylogenetic data, so that the null expectation is a positive correlation between the two variables. The observation of weak and rarely negative correlations between clade density and speciation rates, therefore, cannot be taken as evidence against the presence of an underlying negative diversity-dependence of speciation rate. Moreover, positive diversity-dependence in extinction rate would be imperceptible with such methods.

We entirely agree with Pie [2] that researchers need more empirical evidence to distinguish equilibrium and nonequilibrium (or disequilibrium, see [6]) scenarios. However, we argue that such research requires a sound theoretical framework that enables distinguishing respective processes using clearly formulated hypotheses. Published studies typically test a restricted set of hypotheses, for example, diversification rate versus time for species accumulation (e.g., [7]), and do not allow evaluation of the full spectrum of potential processes. In line with Pie's call for more comprehensive tests of alternative scenarios, we have recently classified the hypotheses on the origin of diversity patterns based on the assumed mutually independent roles of (1) time and (2) speciation rates, so that contrasting predictions based on extant phylogenies and distribution data could be formulated [3] (Box 1). We have shown, using 129 independent clades across tetrapods, that the role of speciation rates was generally negligible, and while the time for species accumulation played some role in younger clades, the equilibrium scenario in which species richness was driven by a balance between region-independent speciation and region- and environment-dependent extinction represented the best-supported scenario of biodiversity dynamics.

This does not mean that all clades reveal equilibrium dynamics. The abovementioned finding that the time for species accumulation matters in younger clades implies that diversity equilibria necessarily comprise only particular phylogenetic scales. However, we disagree with Pie [2] that there is no evidence of a convergence of diversity dynamics at continental and global scales. Although smaller clades often reveal idiosyncratic spatial diversity patterns, larger clades systematically show mutually similar patterns [8], independent of the history of the clades [9], and tightly and predictably linked to environmental productivity [10] and temperature [11]. The finding that various measures of speciation rates and time of species accumulation do not reveal such regular patterns indicates the existence of history-independent diversity attractors (i.e., stable equilibria) at large phylogenetic scales.

Pie [2] rightly pointed to difficulties in testing diversity-dependence, and we have argued [1] that extant phylogenetic trees are not well-suited to such tests. Fossil time series seem more appropriate, but they also suffer from several problems, especially uneven sampling and biases. Additionally, equilibrium dynamics implies a feedback between state variables and respective processes, which hinders using simple correlative approaches—diversity is positively affected by speciation and negatively by extinction, but the diversity-dependence generating equilibria comprises the negative feedback and thus can reverse these relationships (Fig. 1 of [1]). Revealing diversity-dependence thus requires more sophisticated approaches to disentangle the complex causal links. When we applied these methodological tools to available fossil time series, diversity-dependence appeared as a ubiquitous pattern [12]. This does not mean that diversity in all clades is always in equilibrium, but it indicates that the equilibrium framework is useful and its components are falsifiable.

We welcome the discussion about the role of equilibrium dynamics in biodiversity patterns, as we agree that the field is far from settled. Distinguishing equilibrium from out-of-equilibrium states is crucial for our

## Box 1. Testing diversity equilibria and their relevance for macroecology and macroevolution

Equilibrium biodiversity theory can accommodate multiple scenarios of biodiversity dynamics, including scenarios in which diversity is out of equilibrium or equilibrium points are shifting through time. Consequently, such theory is hardly falsifiable as a whole, similar to any general theory (e.g., the theory of evolution). However, it is based on a few key components that can be evaluated, including the negative diversity-dependence of diversification rate and the convergence of species richness across regions with similar conditions and dissimilar histories. Importantly, the framework allows the formulation of contrasting predictions distinguishing equilibrium and disequilibrium processes using phylogenetic and environmental data. Specifically, classical hypotheses about global diversity gradients can be classified into four scenarios based on the importance of time of species accumulation and speciation rate (Figure I). Direct and indirect effects of the surrogates of respective variables (e.g., resource availability estimated using NPP and time using ancestral reconstruction) can then be tested using structural equation models (SEMs) [3]. A concrete theoretical formulation represented by ETBD [1,4] additionally makes testable, falsifiable predictions for species richness, community abundance, extinction, and speciation rates for equilibrium and nonequilibrium communities along environmental gradients.

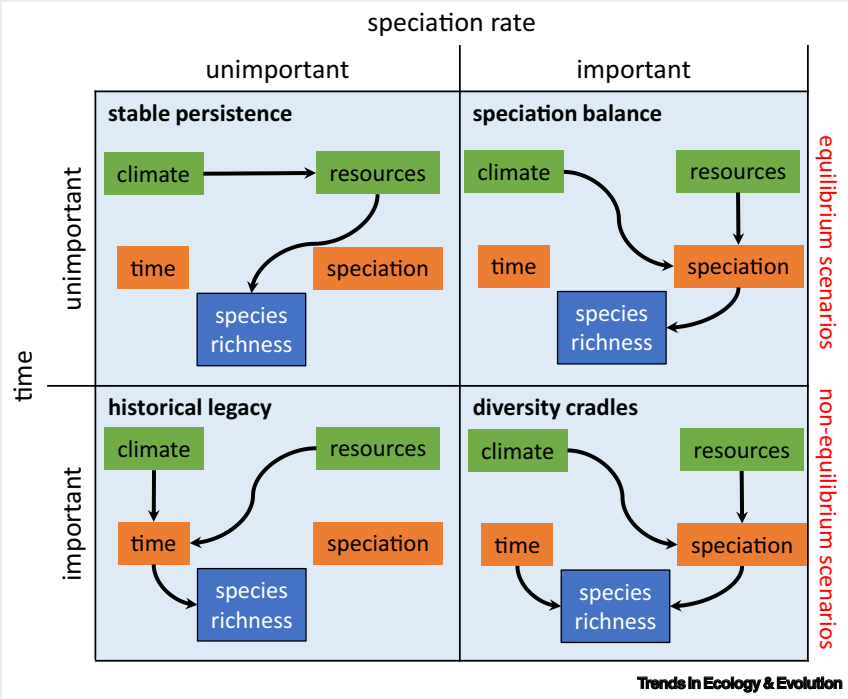


Figure I. Depiction of four scenarios of the origin of spatial diversity patterns, with predicted causal links that can be tested using SEMs and the surrogates of respective variables. Modified from [3].

understanding of the current biodiversity crisis, as well as potential future biodiversity trajectories [6]. However, we argue that there is enough evidence for the existence of biodiversity equilibria and that the Equilibrium Theory of Biodiversity Dynamics (ETBD [4]) provides a consistent framework for hypothesis testing and distinguishing equilibrium and nonequilibrium processes across taxa and regions (Box 1).

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## Declaration of interests

The author declares no competing interests.

[1]Center for Theoretical Study, Charles University and the Czech Academy of Sciences, Prague, Czech Republic
[2]Department of Ecology, Faculty of Science, Charles University, Prague, Czech Republic
[3]School of Earth and Space Exploration, Arizona State University, Tempe, AZ, USA

*Correspondence:
storch@cts.cuni.cz (D. Storch).

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