Biological Theory
https://doi.org/10.1007/s13752-022-00427-9

CRITICAL CONCEPTS IN BIOLOGICAL THEORY

Scaling in the Evolution of Biodiversity

Andrej Spiridonov[1] · **Shaun Lovejoy**[2]

Received: 6 September 2022 / Accepted: 15 December 2022

Abstract
Biodiversity is a fundamental concept in biology. By biodiversity scientists usually mean taxic richness, i.e., the number of species, genera, or other higher taxonomic categories. Diversity sometimes is equated to the complexity of biological systems, but at the higher hierarchical level of observation (in: McShea DW, Brandon RN (2010) Biology's first law: the tendency for diversity and complexity to increase in evolutionary systems, University of Chicago Press, Chicago). Therefore, diversity is a deeply hierarchical concept that can be applied to multiple levels of observation in biology. Here we will concentrate on the problems of the dynamics of taxonomic diversity—the transitive currency of evolutionary, ecological, and developmental biology.

Keywords Court Jester · Crossover · Geophysics · Geo-Red Queen · Macroevolution · Red Queen · Scaling laws

Introduction and History of the Concept

Biodiversity is a fundamental concept in biology. By biodiversity scientists usually mean taxic richness, i.e., the number of species, genera, or other higher taxonomic categories. Diversity sometimes is equated to the complexity of biological systems, but at the higher hierarchical level of observation (McShea and Brandon 2010). Therefore, diversity is a deeply hierarchical concept that can be applied to multiple levels of observation in biology. Here we will concentrate on the problems of the dynamics of taxonomic diversity—the transitive currency of evolutionary, ecological, and developmental biology.

Biodiversity is a product of evolution. Therefore its origin, maintenance, and ultimately dynamics depend on evolutionary mechanisms. There are several models of increasing conceptual complexity that involve different nuances to diversity dynamics: (1) Under the null model of biodiversity change, which is based on the first (or "zero force") law of biology, complexity and diversity at a first approximation should increase due to random mutations and multiscale statistical drift (McShea and Brandon 2010; Brandon and McShea 2020). (2a) In the world of finite space and other resources of a Red Queen (Van Valen 1973), species selection, or more generally species sorting (Gould 2002), prunes the diversity in a perpetual turnover and forces it to converge to some long-term equilibrium. (2b) The universal pattern of declining volatility, which is detectable in a whole range of biological and non-biological entities (Lieberman and Melott 2013), suggests that there could be a trend of stabilization of diversity (its resistance to perturbations) as a side effect of selection of more extinction, and origination-resistant (less "volatile") species. (3) Expansion to new environments, and the origin of new kinds of individuals, and anatomical innovations involve adaptively or at least expansively driven growth in diversity as a result of change in carrying capacity of the biosphere (Benton 1997; Erwin 2012). (4) Unique events exist that cardinally change the qualitative and quantitative nature of the biosphere—the Cambrian explosion is a quintessential example (Gould 1989). (5) Biodiversity dynamics as a random process with effectively infinite number of causal factors, possibly driven by environmental change and a multitude of local biotic changes (e.g., Hoffman 1987; Barnosky 2001; Cornette and Lieberman 2004). In the latter case the structure of biodiversity dynamics should be directly coupled to geophysical

---

✉ Andrej Spiridonov
andrej.spiridonov@gf.vu.lt

Shaun Lovejoy
lovejoy@physics.mcgill.ca

[1] Department of Geology and Mineralogy, Vilnius University, Vilnius, Lithuania

[2] Physics Department, McGill University, Montréal, QC, Canada

dynamics of the planet and possibly even extraterrestrial factors.

This list of mechanisms of macroevolutionary change act over a wide range of timescales, differently affecting behaviors of biodiversity dynamics. The issue of dependency of some observations (in this case diversity) on some independent variable is connected under the rubric of scaling. Before going to the timescaling, we should mention the field of diversity-space scaling, which includes more than a century of research (Rosenzweig 1995). Spatial scaling is described by species-area curves, which usually assume power law relations of a form $D = cA^{z}$, where A is an area, D is a measure of diversity (usually richness of species or genera), c is the intercept, and z is the scaling constant or slope in the log–log space. Various slopes were found for different sized areas and systems, such as islands, regions, or continents, which suggests dominance of different mechanisms (ecological versus evolutionary) at different spatial scales (Rosenzweig 1995).

The scaling of biodiversity in space suggests scaling of biodiversity in time. For example, it was found that diversity levels positively scale on the ecological timescales (up to several decades) in proportion with a measured period of time (Adler and Lauenroth 2003), i.e., the longer time passes the more species can be accumulated in a given area. The scaling (the nature of dependence on the measured timescale) of biodiversity on the evolutionary and especially macroevolutionary timescales is a highly nontrivial matter, as a set of earlier presented models suggest—we can expect different kinds of dynamics, depending on the nature and the dominance of specific evolutionary mechanisms. Are there any long-term outcomes to the evolution of biodiversity? Is evolution characterized by some universal and asymptotic constraints? Especial difficulty in answering these questions poses the open-endedness of the evolutionary process itself (Longo et al. 2012) which changes not only concrete sets of individuals at a particular level, but also the potential to change the nature of the targets of evolution (Maynard Smith and Szathmáry 1998; Godfrey-Smith 2009). Therefore, given the current level of understanding, the best way to answer questions about the fundamental long-term nature of evolutionary dynamics is an empirical analysis of sufficiently detailed global scale and long-term taxonomic data.

The scale-by-scale analyses of macroevolutionary patterns were first enabled by the development of powerful computers and creation of large databases of the durations of Phanerozoic marine animal orders and families, and later genera by Sepkoski and his associates in the early 80s and 90s (Sepkoski et al. 1981; Sepkoski 2012), which built on earlier work such as that of Newell (1963). The classical approach for this problem is the use of Fourier transforms in estimating spectra of key macroevolutionary variables, such as origination, extinction, and turnover rates or biodiversity levels. These approaches historically were usually applied toward extraction, characterization, and testing of timescale-specific features, such as periodicities in extinction rates (Raup and Sepkoski 1984; Lieberman and Melott 2007, 2012) and their association with the major global-scale geological drivers (Roberts and Mannion 2019). Although, there was a significant flash of interest toward characterization of statistical features of macroevolutionary dynamics, based on the estimation of spectral slopes of extinction statistics (Newman and Palmer 2003), which searched for universal behaviors such as self-organized criticality (SOC) (Solé et al. 1999) or stochastic multiplicative multifractals (Plotnick and Sepkoski 2001).

Biodiversity Scaling in the Light of Current Knowledge

Advances in the development of numerical analysis techniques of scaling geophysical processes now allow accurate quantitative and qualitative characterization of timescale-dependent behaviors (Lovejoy and Schertzer 2012). The best way to characterize so-called "structure functions" (dependence of typical fluctuation amplitudes as a function of measured timescale) is to use the so-called Haar fluctuation—historically the first proposed wavelet (Haar 1910). Structure function has the form $\langle |\Delta T|_{Haar} \rangle \propto \Delta t^{H}$; here H is a – measurement timescale-dependant fluctuation (scaling) exponent which is defined with respect to typical (mean absolute) fluctuation. If the fluctuation exponent $H > 0$, this shows that the process is "wandering," and shows trend-like behavior; otherwise if $H < 0$, then the process is "stabilizing"—here time series become more and more similar with the increase of sizes of the measured intervals Δt.

We applied this fluctuation analysis technique to the evolution of marine animal genus-level biodiversity dynamics through the Phanerozoic eon in order to test two possible mechanisms of change, which envision fundamentally different scaling behaviors of biodiversity dynamics (Spiridonov and Lovejoy 2022). The two most viable and widely discussed hypotheses of the fundamental nature of biodiversity dynamics are: (1) the Red Queen world (model number 2 from the first section) which envisions equilibration due to competition and negative feedbacks or negative population density dependence; (2) and the so-called Court Jester world (model number 5 from the first section)—in this case diversity dynamics inherits whether scaling is exhibited by the external or geophysical systems that drive it. We should note that the Red Queen hypothesis in a narrow sense (constancy of extinction due to constant negative biotic feedbacks in biota) is currently a controversial one, especially as applied to macroevolutionary timescales (Strotz et al. 2018). Therefore, here we understand the Red Queen in a very broad sense—as any negative dependence of extinction and origination rates on taxonomic diversity levels (density of biota).

The results of our study revealed that there are two qualitatively different regimes of global marine animal biodiversity dynamics: at timescales shorter than 40 million years, the diversity dynamics exhibits a diverging or wandering nature with a positive fluctuation exponent (H = +0.25); on the other hand, at longer timescales it is characterized by a negative scaling exponent (H = −0.25). The megaclimate—the global temperature variational regime at timescales longer than one million years—is also characterized by a positive fluctuation exponent up to the longest measured timescales of hundreds of millions of years, now estimated to have the same values as for "short-term" diversity dynamics H = +0.25 (Spiridonov and Lovejoy 2022). This same scaling pattern of paleoclimate and diversity, and also additional correlational evidence, revealed that the biodiversity dynamics can be described as obeying a Court Jester model of environmental forcing on shorter macroevolutionary timescales—up to 40 million years, where variability reaches its maximum (Fig. 1). After this threshold timescale it starts another—a self-regulating regime, while the megaclimate continues to be more and more unstable with longer timescales. Therefore, at timescales longer than 40 million years the scaling pattern of diversity dynamics becomes radically different from that of megaclimate. This break in patterns shows the transition of biodiversity dynamics towards more and more autonomy from the environmental variations, controlled by *life* itself—the Red Queen, or more precisely Geo-Red Queen regime, since in our explanation plate tectonics plays a crucial role in mixing biota and thus enabling planetary-scale self-regulation of macroevolution (Spiridonov and Lovejoy 2022). Therefore the history of life on Earth is a mixture of two qualitatively different dynamical processes described by different scaling laws—the evolution of life acts as a passive consequence (driven process) of geophysical processes up to the critical timescale of 40 million years; and at longer timescales the effective globalization by means of the mixing of biota starts to dominate, and induces stabilization and self-regulation.

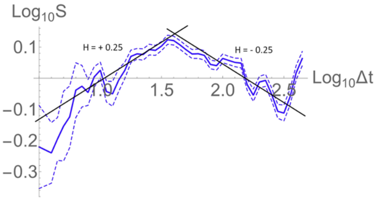

Fig. 1 Scaling of marine animal diversity dynamics (Spiridonov and Lovejoy 2022) in the Phanerozoic with reference lines showing approximate slopes of scaling exponents (H). X-axis shows measured timescales in $\log_{10}$ million years. On the y-axis diversity is expressed in numbers of genera × 0.001. The break between scaling patterns (crossover of the Court Jester and the Geo-Red Queen regimes) is evident at approximate timescale of 40 million years (1.6 on the log scale)

There could be another explanation for the stabilization of diversity dynamics at the global scale and long timescales though. This mechanism is the sorting of species and higher taxa, with survival of groups with lower volatility (Lieberman and Melott 2013). The mechanism envisions the decreasing amplitudes of diversity fluctuations with the passage of time. The decreased origination and extinction probabilities would result in the inertia of the standing diversity to these perturbations. Surviving clades become more inert, less prone to perturbations by external or internal factors that can lead to speciation or extinction events. Therefore the appearance of equilibrium on the longest timescales can appear as time passes—and therefore diversity stabilization should be expected with passing time as well as with the measurement timescales. Although such a pattern is possible under declining volatility conditions, current evidence does not show a pattern of decreased fluctuations of global diversity with passing time. On the contrary, one of the most conspicuous features of marine Phanerozoic diversity—the Cenozoic diversity maximum (see, for example, Spiridonov and Lovejoy 2022)—appeared late in the history of complex life. This example shows that the probable decreases in absolute amplitudes of originations and extinctions (decrease in volatility of macroevolution) aren't sufficient for achieving stability. Even small sustained imbalances (incoherences) in origination and extinction rates can result in very large fluctuations of diversity in the long run (at deca-million-year timescales). This is what we've found earlier (Spiridonov and Lovejoy 2022), that the correlations between origination and extinction rates as well as typical magnitudes of fluctuations become coherent and correlated just at the longest timescales, greater than 40 Myr. Therefore, as current data suggest, the diversity self-regulation at the longest timescales is the most probable explanation of the stabilizing pattern of negative diversity scaling at scales > 40 Myr. Clearly we need more thorough tests of these two alternative mechanisms responsible (to a different degree) for the stabilization of diversity on the longest timescales.

A multiplicative stochastic multifractal simulation parameterized on the scaling laws of global marine animal biodiversity dynamics (Fig. 2) shows that we should expect trend-like (wandering) features on timescales up to several hundred million years due to the unstable nature of "short-term" dynamics. Therefore, in this view, if we had a much longer run of biodiversity change, we should have seen many grand (long-term and large magnitude) features, such as Meso-Cenozoic diversity increase of genera, which is found in the empirical data. In the view of our model, these deca- to deci- million scale trends are transient features, which in the real world are generated by global circumstances of

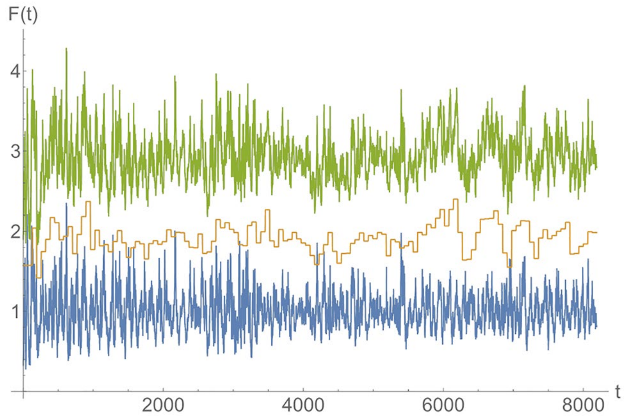

Fig. 2 A generic multifractal simulation which is parameterized by the diversity dynamics of Phanerozoic marine animal genera (Spiridonov and Lovejoy 2022). It shows a mixed dynamics—"wandering" at short timescales, and stabilizing at longest timescales. Time is arbitrary. Parameters of the multifractal model (for further details see Lovejoy and Schertzer 2013): $C_1 = 0.02$, $\alpha = 1.8$ (low intermittency), length of the time series $2^{13} = 8192$ points; transition between wandering and stabilizing regimes happens at the scales of $2^6 = 64$ points. Top is the sum of wandering and stabilizing dynamics. Middle is low passed dynamics with scaling exponent ($H = -0.25$) as in the "long-term" $\Delta t > 40$ million years macroevolutionary dynamics—it shows stabilizing or relaxing with increasingly longer timescales behavior. The bottom is high passed simulation with the same scaling exponent ($H = +0.25$) as the "short-timescale" $\Delta t < 40$ million years macroevolutionary dynamics—it shows "wandering" behavior, also typical for the megaclimate regime (Lovejoy 2015). If we scale the current simulation to the geological time, it shows how Phanerozoic diversity dynamics could have looked through a duration of 5.12 billion years, assuming that the negative scaling regime further continues in to the billion-year timescales. It can be seen that at scales up to several hundred million years "trends," such as the Cretaceous-Cenozoic diversity increase determined in the empirical data (Spiridonov and Lovejoy 2022), can appear as a consequence of wandering behavior of shorter-scale processes

megaclimate and tectonic states (Spiridonov and Lovejoy 2022).

Implications for Biological Theory

The scaling is timescale symmetry—it connects the large and small scales in scale-free power law manner (Lovejoy 2022), it reveals the uniformity of a mechanism in a scaling range, and it also shows the fundamental nature of the process if we know the sign and value of the scaling exponent H. Therefore, knowing that the megaclimate scales positively ($H = +0.25$) from timescales of millions to hundreds of millions of years, and that diversity also scales positively ($H = +0.25$) up to a 40 Myr timescale and later scales negatively ($H = -0.25$), reveals many significant things not only about how life evolves but also about its relationship with the planet on a range of long timescales. The fact that life and megaclimate scale positively unambiguously shows that there is no stabilization of the climate by life or any other mechanism at scales > 1 Myr. Similarly life also does not show stabilization at the global scale up to timescales longer than 40 Myr. Therefore the Gaia hypothesis which envisions the optimization of life's environment by life itself by means of ecological and evolutionary change isn't supported by evidence (Spiridonov and Lovejoy 2022). If the Gaia world were the case, then we should have been observing negative scaling exponents from the shortest timescales to the longest ones.

Although currently the presented scaling approach to paleobiological dynamic patterns is a new one, we performed yet another study which tried to explain the dynamics of geographic ranges of brachiopod genera through Phanerozoic. This study revealed that the shapes of geographic ranges scale positively with measured timescales, and thus do not show signs of stabilization, following similarly positively scaling patterns of global continental fragmentation states (Spiridonov et al. 2022). Since geographic ranges often determine fitness of taxa—that is, their origination and extinction rates (Jablonski 1987, 2008)—this observation additionally supports the principal importance of global unstable positively scaling geophysical processes in determining the qualitative and quantitative nature of macroevolutionary dynamics at long timescales. Although there is nuance here. Since extinction and origination rates show negative scaling ($H = -0.25$), and they are negatively correlated with diversity levels, the density dependency of macroevolutionary rates on diversity levels becomes more important at long timescales (Spiridonov and Lovejoy 2022), and despite larger and larger perturbation caused by tectonic changes, their effects on macroevolution, due to this internal stabilization, become, relatively speaking, smaller and smaller with scale. Therefore, the presented picture differs from previous models (such as a logistic model) which assume constancy of density dependence at all scales (such as Sepkoski 1981); our analysis shows that its effects are apparent at the global spatial scales on timescales longer than 40 Myr. Therefore, currently presented patterns and the underlying model do not assume convergence of diversity in time (since at no time will we find unchanging asymptotic numbers of taxa) but the convergence of diversity at long *timescales*.

We should note that the case of density regulation on the longest timescales is quite clear (Spiridonov and Lovejoy 2022): (1) extinction and origination rates are scaling negatively at all timescales, which implies their regulation (or cancelling behavior); (2) at timescales > 40 Myr diversity also exhibits negative scaling—a tendency to converge on a long-term average; (3) at long timescales (> 40 Myr) extinction and origination rates are correlated negatively with the diversity (prima facie evidence of negative rate dependence (stabilization) on diversity levels); (4) scale by scale relations of typical amplitudes of origination and extinction rates become similar after crossover timescale of 40 Myr—their long timescale dynamics become coherent; (5) extinction and origination rates become strongly correlated after crossing 40 Myr timescales, which also suggests their biotic regulation and synchronization, which results in equilibrial dynamics; (6) finally, there is monotonous decrease in correlations between diversity and temperatures with longer timescales, which shows autonomization of biota, and start of dominance of other (as evidence shows, internal) factors.

The view presented based on the idea of wide-range scaling of temperature, extinction, origination, diversity, tectonics, temperature, and sea level (and probably more crucial variables) is that the fundamental macroevolutionary and physical processes are scaling, but since they scale at different rates (different exponents), there may be "crossover" scales where one dominates another, as in the case of diversity dynamics where, in our view, positively scaling stabilizing density dependence of macroevolutionary rates overwhelms the effects of positively scaling Earth system processes on the same rates.

The described cases show that the empirically estimated scaling laws could be used in determining basic structural dynamic properties of evolutionary systems, and their driving or interacting external mechanisms, in this way using a given approach in mechanistic model generation, selection, and optimization. So far, the temporal scaling of biodiversity dynamics has been explored at the global scale and with marine animal genera. Many other applications, including the exploration and testing of mechanisms of spatiotemporal evolutionary dynamics (e.g., Eldredge et al. 2005) will undoubtedly resolve many questions on the tempos and modes of macroevolutionary change. Formulation of hypotheses of macroevolutionary change in mathematical terms can reveal what kind (if any) of scaling behavior given mechanisms are predicting. Therefore, we argue that similarly to its use in the atmospheric sciences (Lovejoy and Schertzer 2013; Lovejoy 2019), scaling could be the unifying nomothetic theme used in revealing statistical laws (in the spirit of Gould 1980, 2002; Raup and Gould 1974; and more recently Lieberman 2016), using which we can make robust descriptions, while ignoring myriads of idiosyncratic details of many lower-level structures, therefore making the field of macroevolution not only testable, and explainable, but also predictive on many spatial and time scales.

Acknowledgments We would like to thank Kenneth McKenna and Stuart Newman for the opportunity to contribute this essay. We also thank Bruce Lieberman for many suggestions which significantly improved and clarified the essay.

Funding The research of A. Spiridonov was supported by the Research Council of Lithuania project S-MIP-21-9 "The role of spatial structuring in major transitions in macroevolution." S. Lovejoy acknowledges the National Science and Engineering Council of Canada for support.

Declarations

Conflict of interest The authors declare no conflicts of interests that hinder the publication or review of the article.

References

Adler PB, Lauenroth WK (2003) The power of time: spatiotemporal scaling of species diversity. Ecol Lett 6:749–756

Barnosky AD (2001) Distinguishing the effects of the Red Queen and Court Jester on Miocene mammal evolution in the northern Rocky Mountains. J Vertebr Paleontol 21:172–185

Benton MJ (1997) Models for the diversification of life. Trends Ecol Evol 12:490–495

Brandon RN, McShea DW (2020) The missing two-thirds of evolutionary theory. Cambridge University Press, Cambridge

Cornette JL, Lieberman BS (2004) Random walks in the history of life. Proc Natl Acad Sci USA 101:187–191

Eldredge N, Thompson JN, Brakefield PM, Gavrilets S, Jablonski D, Jackson JBC et al (2005) The dynamics of evolutionary stasis. Paleobiology 31:133–145

Erwin DH (2012) Novelties that change carrying capacity. J Exp Zool B Mol Dev Evol 318:460–465

Godfrey-Smith P (2009) Darwinian populations and natural selection. Oxford University Press, Oxford

Gould SJ (1980) The promise of paleobiology as a nomothetic, evolutionary discipline. Paleobiology 6:96–118

Gould SJ (1989) Wonderful life: the Burgess Shale and the nature of history. WW Norton, New York

Gould SJ (2002) The structure of evolutionary theory. Harvard University Press, Cambridge

Haar A (1910) Zur theorie der orthogonalen funktionensysteme. Math Ann 69:331–371

Hoffman A (1987) Neutral model of taxonomic diversification in the Phanerozoic: a methodological discussion. In: Nitecki MH, Hoffman A (eds) Neutral models in biology. Oxford University Press, New York, pp 133–146

Jablonski D (1987) Heritability at the species level: analysis of geographic ranges of *Cretaceous mollusks*. Science 238:360–363

Jablonski D (2008) Species selection: theory and data. Annu Rev Ecol Evol Syst 39:501–524

Lieberman BS (2016) Pattern versus processes and hierarchies: revisiting eternal metaphors in macroevolutionary theory. In: Eldredge N, Pievani T, Serrelli E, Temkin I (eds) Evolutionary theory: a hierarchical perspective. University of Chicago Press, Chicago, pp 29–46

Lieberman BS, Melott AL (2007) Considering the case for biodiversity cycles: re-examining the evidence for periodicity in the fossil record. PLoS ONE 2:e759

Lieberman BS, Melott AL (2012) Whilst this planet has gone cycling on: what role for periodic astronomical phenomena in large-scale patterns in the history of life? In: Talent JA (ed) Earth and life. International year of planet earth. Springer, Dordrecht, pp 37–50

Lieberman BS, Melott AL (2013) Declining volatility, a general property of disparate systems: from fossils, to stocks, to the stars. Palaeontology 56:1297–1304

Longo G, Montévil M, Kauffman S (2012) No entailing laws, but enablement in the evolution of the biosphere. In: Proceedings of the fourteenth international conference on Genetic and evolutionary computation conference companion. ACM, pp 1379–1392

Lovejoy S (2015) A voyage through scales, a missing quadrillion and why the climate is not what you expect. Clim Dyn 44:3187–3210

Lovejoy S (2019) Weather, macroweather, and the climate: our random yet predictable atmosphere. Oxford University Press, New York

Lovejoy S (2022) Scaling and scale invariance. In: Daya SB, Cheng Q, McKinley J, Agterberg F (eds) Encyclopedia of mathematical geosciences. Encyclopedia of earth sciences series. Springer, Cham, pp 1–13

Lovejoy S, Schertzer D (2012) Haar wavelets, fluctuations and structure functions: convenient choices for geophysics. Nonlinear Process Geophys 19:513–527

Lovejoy S, Schertzer D (2013) The weather and climate: emergent laws and multifractal cascades. Cambridge University Press, Cambridge

Maynard Smith J, Szathmáry E (1998) The major transitions in evolution. Oxford University Press, Oxford

McShea DW, Brandon RN (2010) Biology's first law: the tendency for diversity and complexity to increase in evolutionary systems. University of Chicago Press, Chicago

Newell ND (1963) Crises in the history of life. Sci Am 208(2):76–95

Newman M, Palmer R (2003) Modeling extinction. Oxford University Press, Oxford

Plotnick RE, Sepkoski JJJ (2001) A multiplicative multifractal model of originations and extinctions. Paleobiology 27:126–139

Raup D, Gould SJ (1974) Stochastic simulation and evolution of morphology-towards a nomothetic paleontology. Syst Biol 23:305–322

Raup D, Sepkoski J (1984) Periodicity of extinctions in the geologic past. Proc Natl Acad Sci USA 81:801–805

Roberts GG, Mannion PD (2019) Timing and periodicity of Phanerozoic marine biodiversity and environmental change. Sci Rep 9:1–11

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge

Sepkoski JJ (1981) A factor analytic description of the Phanerozoic marine fossil record. Paleobiology 7(1):36–53

Sepkoski D (2012) Rereading the fossil record: the growth of paleobiology as an evolutionary discipline. University of Chicago Press, Chicago

Sepkoski JJ, Bambach RK, Raup DM, Valentine JW (1981) Phanerozoic marine diversity and the fossil record. Nature 293:435–437

Solé RV, Manrubia SC, Benton M, Kauffman S, Bak P (1999) Criticality and scaling in evolutionary ecology. Trends Ecol Evol 14:156–160

Spiridonov A, Lovejoy S (2022) Life rather than climate influences diversity at scales greater than 40 million years. Nature 607:307–312

Spiridonov A, Balakauskas L, Lovejoy S (2022) Longitudinal expansion fitness of brachiopod genera controlled by the Wilson cycle. Glob Planet Change 216:103926

Strotz LC, Simões M, Girard M, Breitkreuz L, Kimmig J, Lieberman BS (2018) Getting somewhere with the Red Queen: chasing a biologically relevant definition. Biol Lett 14(20170734):1–7. https://doi.org/10.1098/rsbl.2017.0734

Van Valen L (1973) A new evolutionary law. Evol Theory 1:1–30