

Review

Cite this article: Spiridonov A, Eldredge N (2024). The Bretskyan hierarchy, multiscale allopatry, and geobiomes—on the nature of evolutionary things. *Paleobiology* 1–20. <https://doi.org/10.1017/pab.2023.37>

Received: 11 July 2023
Accepted: 20 November 2023

Corresponding author:
Andrej Spiridonov;
Email: andrej.spiridonov@gf.vu.lt

The Bretskyan hierarchy, multiscale allopatry, and geobiomes—on the nature of evolutionary things

Andrej Spiridonov¹  and Niles Eldredge²

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

²Division of Paleontology, American Museum of Natural History, New York, New York, U.S.A.

Non-technical Summary

Evolution works through the interaction of ecology and genealogy in time and space. Ecological hierarchy describes processes of energy and matter transfer, while genealogical hierarchy describes patterns of genetic heritability at many scales. Here a new and hybrid in nature, eco-genealogical Bretskyan hierarchy is described. Basic units of this hierarchy are spatially and temporally distinct portions of biota. Proximity of organisms and taxa in space and time enables their coevolution and integration. Lower tiers of this hierarchy are occupied by holobionts—organism-like communities; while at higher tiers, this hierarchy occupied by what are called here geobiomes—local and regional biotas and embedding geosystems that evolve in tandem and exist on geological time scales. The largest rank in the Bretskyan hierarchy is the global biota—Gaia herself. Geobiomes described here are evolutionary individuals with beginnings and ends and defined spatial ranges. The individuality of geobiomes is defined by geological barriers. Barriers form at all time and space scales, and because larger barriers last longer, geobiomes are more individuated at larger spatial scales. The structure of a planet is imposed on biota. Here we present a theoretical framework on how we should understand this geologically imposed structuring, which determines the spatial extents and durations of coevolution and integration and disintegration of biotas, as well as their transformation in time and space.

Abstract

The process of evolution and the structures it produces are best understood in the light of hierarchy theory. The biota traditionally is described by either the genealogical Linnaean hierarchy or economic hierarchies of communities or ecosystems. Here we describe the Bretskyan hierarchy—a hybrid eco-genealogical hierarchy that consists of nested sets of different-sized, usually polyphyletic communities of interacting individuals separated from other such communities in space and time at multiple scales. The Bretskyan hierarchy consists of elements that have both genealogical and economic properties and functions—situated between, and connecting the elements of, the economic hierarchies (Vernadskyan) and the genealogical (Linnaean) hierarchy. The described hierarchy at lower tiers is populated by holobionts, individuals composed of multiple polyphyletic lineages integrated by functional interactions or biotically fabricated structures, such as membranes. At larger spatial tiers and longer time scales, the members of the Bretskyan hierarchy are of a more diffuse nature, partially due to the small size and relatively short duration of us as observers of larger and longer-lasting structures, here described as geobiomes. Their individuality is externally forced and directly tied to the spatial and temporal physical structures of our planet. These are sub-bioprovinces and bioprovinces—large and effectively isolated spatiotemporal structures of biota integrated internally by coevolution and individuated externally by a hierarchy of barriers. Gaia is here understood as the largest eco-genealogical individual compartmentalized by the outer space of the Earth and integrated at long time scales by biotic interactions and plate tectonic mixing of biota. The existence of a hierarchy of barriers and multilevel allopatry suggests that geographic isolation takes part not only in individuating species lineages, but also in producing coherent complexes of separate lineages forming bioprovinces at multiple space and time scales. The sizes, configurations, and durations of Bretskyan units are directly tied to geodynamics, demonstrating the central role of the physical planet in the processes of individuation and merging of geobiomes and the control of coevolution, and all its ramifications, at multiple space and time scales. The Bretskyan hierarchy also allows the integration of previously unconnected themes—“egalitarian” major transitions in individuality (e.g., eukaryogenesis) and some of the megatrazjectories in the history of life—into a single theoretical framework of spatial and temporal scaling of eco-genealogy. The pervasive scaling of geodynamical processes and the direct connection of geodynamics to the dynamics of Bretskyan units allows us to formulate conjectures on the scales and limits of spatial and temporal contingency and competitiveness of biotas in evolution.

© The Author(s), 2024. Published by Cambridge University Press on behalf of Paleontological Society. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

PALEOBIOLOGY
A PUBLICATION OF THE
 PALEONTOLOGICAL SOCIETY

 **CAMBRIDGE**
UNIVERSITY PRESS

Introduction

Evolutionary theory is in perpetual search for the unifying principles that can increase its scope in the realm of objects, structures, and patterns and deepen understanding of underlying processes (Gould 1980, 1985, 2002; Eldredge 1995). The biological world is usually conceptualized in one of two ways: either as a perpetually branching tree forming the Linnaean hierarchy of taxa—genealogically nested individuals; or as the hierarchy of ecosystems or communities that are tied together by changes in abundance and consequently in energy and matter transfer. The genealogical or Linnaean part of hierarchical evolutionary theory has achieved significant conceptual, mathematical, and empirical progress on the meaning, scope, and significance of multilevel selection or sorting and cross-level effects in evolution and emergence of individuals (Lewontin 1970; Eldredge and Gould 1972; Stanley 1975, 1979; Eldredge and Salthe 1984; Vrba and Eldredge 1984; Eldredge 1985, 1989, 1996; Salthe 1985; Vrba and Gould 1986; Lloyd and Gould 1993; Lloyd 1994; Maynard Smith and Szathmáry 1998; Gould and Lloyd 1999; Lieberman and Vrba 2005; Okasha 2006; Jablonski 2007, 2017). The economic side of biology is also recognized as having hierarchical structure (Allen and Starr 1982; Eldredge and Salthe 1984; Eldredge 1985; Leibold et al. 2004; Holyoak et al. 2005; Bennington et al. 2009; Tomašových and Kidwell 2010), connected in many nontrivial ways to the genealogical hierarchy and through the feedbacks forming the eco-genealogical dynamics (Eldredge 1985, 1999, 2003; Van Valen 1989; Vrba 1993; Lieberman et al. 2007; Stigall 2015; Tëmkin and Eldredge 2015); for a recent review of the “dual hierarchy approach,” see Rosenberg (2022). The economic side of biology can be further understood in two competitive hierarchical ways that are mirrored by the institutional subdivisions in ecology and Earth sciences: as a hierarchy of interacting populations forming nested communities of different sizes (population ecology/paleoecology view) or as a hierarchy of energy–matter and biogeochemical processes (ecosystem ecology and geobiology view) that form functional components nested in ever larger ecosystems (O’Neill et al. 1986). Therefore, the biological realm can be seen as multidimensional hierarchy, where scalar unidimensional projections were named genealogical, community, and ecosystem hierarchies.

In parallel to the development of hierarchical theories of processes working on genealogical and economic hierarchies, the hybrid Bretskyan hierarchy arises (named after paleoecologist Peter W. Bretsky [Eldredge 1985]) from the growing understanding of symbiogenesis, with the recognition of multi-taxa collectives forming individual-like “holobionts” that can act as units of selection (Roughgarden et al. 2018). Here holobionts are understood as cross-genealogical entities that form hierarchically nested genealogy-like patterns across a range of time scales. Eukaryotic cells (Margulis and Bermudes 1985; Margulis et al. 2005) and specialized coalitions of lipid membranes, proteins, and nucleic acids were stepping stones in the emergence of more complex life-forms (Maynard Smith and Szathmáry 1998; Takeuchi and Kaneko 2019). The emergence of replication and life itself from competing and cooperating chemical reactions also in some sense has polyphyletic/holobiont-like qualities (Maynard Smith and Szathmáry 1998; Nowak and Ohtsuki 2008; Calcott and Sterelny 2011). Therefore, the theme of community evolution and individuality, connected by the common terms of “holobionts” and “symbiosis,” clearly reveals its own hierarchy of entities: networks and coalitions of replicating molecules, integrated unicellular aggregates,

and polyphyletic and functionally integrated multicellular organisms form at least three such levels of many. Lateral gene transfer also shows the importance of spatially and temporally proximal interaction between distant clades in forming patterns in phylogeny and individuality distinct from classical treelike structures (Bapteste et al. 2012). The importance of evolution of ecosystems and communities clearly suggests the need for reconceptualization of evolutionary biology (Aarssen and Turkington 1983; Van Valen 1991; Lekevičius 2006; Bouchard 2014), along with the introduction of explicitly hierarchical concepts (de Castro and McShea 2022).

When developing the dual hierarchical theory of economic and genealogical systems, one of us made a suggestion: “The ecological and genealogical histories of life can be properly viewed as strongly linear or as various hierarchically arranged patterns—such as the taxic (Linnaean) and homology hierarchies, plus the unnamed historical hierarchy of ecological systems—which we may, with some justification, label the Bretskyan hierarchy” (Eldredge 1985: p. 176). Back then, the hierarchy of ecosystems was classified as a function of spatial scale and consequently functional inclusivity, and that is how it has remained understood in most subsequent macroecological and biogeographic studies (Brown 1995; McGill et al. 2019). The evolution of life happens not only in time but also in space (Willis 1922). The historical (temporal) structure and its connection to the spatial scales of the Bretskyan hierarchy have yet to be fully formulated to this day.

Here we present a theory explaining the properties of the Bretskyan hierarchy of spatial and temporal units of biota called here holobionts and geobiomes—genealogically significant units internally integrated by spatiotemporal proximity, common biogeochemical cycles, and geologically caused compartmentalization, and explain their role in evolution, in the context of spatial and temporal scaling of dynamics of occupied space through the entire range of time scales (Table 1). If the matter/energy and information transfer functions are in the same system—that makes that system a Bretskyan unit.

This work is the continuation of the dual hierarchy approach toward conceptualizing the biological world (Eldredge and Salthe 1984; Eldredge 1985, 1986, 1989; 1996). The explanatory power of the dual approach is based on the apparent dichotomy of information transfer (“fate of transmissible information”) and matter/energy transfer processes that enable a living system to actually be “alive.” Here we show that spatial proximity and the isolating nature of geological barriers fragment portions of biota in space and time, which yields a nontrivial consequence for the structure and function of the biological world—external forcing of individuality (or emergence of “effect individuality”). This hierarchy of geological structures controls not only individuality of hierarchically structured parts of biota, but also patterns, scales, and durations of coevolution. This observation calls for the definition of a conceptually new (hybrid in nature) hierarchy of eco-genealogical units (having similarities to “maker hierarchy” in cultural evolution [Eldredge 2009]), which are defined by their spatial and temporal separateness, their genealogical significance, and their internal binding coevolution between living and nonliving surrounding systems. The Bretskyan hierarchy is, in effect, the real-world “suture zone” between the ecological and genealogical realms—as epitomized by the dual nature of individual organisms.

The Bretskyan hierarchy—which can also be called Vrba’s hierarchy, or Brett’s or even d’Orbigny’s or Cuvier’s hierarchy, as they all recognized discreteness of fossil biotas in space–time

Table 1. Classification of characteristics of ecosystem, community, Linnaean (genealogical), geological time scale/paleogeography, and Bretskyan (holobiont-geobiome) scalar hierarchies (sensu Salthe 1991) and their elements. The discussed features of hierarchies are based on previous works (Eldredge and Salthe 1984; Vrba and Eldredge 1984; Eldredge 1985, 1996; Salthe 1985; O’Neill et al. 1986; Ogg et al. 2008; Miall 2010; Torsvik and Cocks 2016) and the current theory.

Quality/ type of hierarchy	Economic/functional		Linnaean/ genealogical	Bretskyan/ holobiont-geobiome	Hierarchy of geological structures/geological time scales
	Ecosystem	Community			
Elements of hierarchy	Molecules and abiotic and biotic chemical reaction networks; biological units transforming and transporting energy and matter (producers, consumers, etc.)	Depending on the level: 1. functional molecules (e.g., enzymes); 2. different types of cells in unicellular communities or in multicellular organisms; 3. organisms (in a broad sense of the word) assigned to species or morphs	Nucleic acids (DNA and RNA), their higher-order intracellular or extracellular structures (genes, plasmids, chromosomes, viruses); nuclei, mitochondria; nucleic acids carrying cells; organisms; monophyletic groups or colonies; species; clades.	Chemical reaction networks possessing both functional and reproductive capacities; cells and organisms (as monophyletic and composed from many historically distinct units); local, regional, and global biotas. Depending on the level of integration units can be called either holobionts (high integration) or geobiomes (lower integration), with these categories existing in a continuum	Planetary structures of all scales: mostly observable as structures of Earth’s crust and presented in form of paleogeographic/tectonic maps or stratigraphic charts Temporal dimension of the hierarchy represented by units of geological time scales of different spatial and temporal inclusivity
Space	Essential in definition of boundaries of units and a defining feature of hierarchy (metaecosystems include spatial subsets of smaller ecosystems)	Essential in definition of boundaries of units and a defining feature of hierarchy (metacommunities include spatial subsets of smaller communities and are parts of bioprovinces)	Absent from the definition of units.	Essential in definition of boundaries of units and a defining feature of hierarchy	Essential in defining structures of the planet by means of stratigraphic and structural geological subdivision and grouping
Time	Absent or plays a secondary role in definition of a unit	Absent or plays a secondary role in definition of a unit	Acknowledged implicitly as a correlate of the branching order	Essential in definition of boundaries of units and a defining feature of hierarchy	Essential, with time subdivisions produced by defining significant transitions in planetary and more local history—including biological history
Function	Explicitly functional	Explicitly or implicitly functional	Nonfunctional	Explicitly or implicitly functional	Explicitly functional (essentially all physical, chemical, and biological changes) and also defining boundary conditions for dynamics of other discussed function-laden hierarchies
Heritability	Undefined or having a limited role	Undefined or having a limited role	The defining feature	Explicitly acknowledged; one of the defining features	Appears as the inertia of persistence of geological, biological, and other significant structures Has a special role in tracing changes in continental individuality (an example of such pedigree: Laurentia → Laurussia → Pangaea → Laurasia → North America)

and the importance of physical forcing—is a departure from the more abstract or “pure” genealogical (Linnaean) and ecological/economic (Vernadskyan) hierarchies, toward a hierarchy grounded in real-world geobiological systems characterized by both functionality and heritability—the hierarchy of holobionts and geobiomes. The realization of this new hierarchy opens new avenues of integration of geological and biological sciences in a causally and ontologically explicit framework that produces a number of predictions and explains many disparate patterns observed earlier.

Connections between Community, Ecosystem, Linnaean, “Geological Time Scale,” and Bretskyan Hierarchies

The Linnaean or genealogical hierarchy has received considerable interest in debates on the levels of selection, and evolution more generally (Vrba and Gould 1986; Lloyd 1994; Gould and Lloyd 1999; Gould 2002; Okasha 2006, 2012; Simpson 2011). One of the major discussion points is where we should find the focus of selection processes, and which entities are selected and which are sorted or receiving side effects of selection events (Eldredge 1996; Jablonski 2008b). In any case, the Linnaean hierarchy, even though reticulated by myriad hybridization and lateral gene transfer events (Arnold 2006), shows a distinct treelike structure and represents a hierarchy of informational inheritance. The economic hierarchy is more complicated, because (1) it can be represented as a hierarchy of interacting populations and communities (Eldredge 2008), or (2) alternatively, it can be seen as a hierarchy of ecosystems (O’Neill et al. 1986). The ecosystem view is even more complex, because it also encompasses abiotic energy and matter transfer, which are tied to geological processes that span many time scales and interact not only horizontally (in geographic space of longitude [λ] and latitude [φ] but also in the third dimension [z] across all planetary spheres—crust, mantle, and core). There is no doubt that, at the long time scales of thousands to billions of years, life is an integral part of the Earth’s dynamics, with feedbacks working in both directions and most clearly apparent on time scales longer than millions of years (Lovejoy 2015; Wignall 2015; Knoll and Nowak 2017; Spiridonov et al. 2017c, 2022; Eichenseer et al. 2019; Anderson 2022; Sánchez-Baracaldo et al. 2022; Spencer et al. 2022; Spiridonov and Lovejoy 2022, 2023). Therefore, the hierarchy of ecosystems, and especially the dynamics of their spatial and compositional structure on long time scales, should be understood as a part of the geological/intra-planetary hierarchy of processes and structures. The Bretskyan hierarchy traces fates and spatial configurations of component populations of interacting functional and genealogical collectives. It combines approaches of all major biological hierarchies—community hierarchy of biotic functional interactions, ecosystem hierarchy of Earth–life interactions, and genealogical hierarchy of patterns of information transfer.

To distinguish the functional hierarchy of biocoenoses (Tëmkin 2021), which we here call the Vernadskyan hierarchy, from the historical hierarchy of eco-genealogical groupings, we present here a reassessed Bretskyan hierarchy (Table 1). The Bretskyan units are formed by proximately interacting biota co-occurring in contingently determined time and space. The fact that most Bretskyan units are polyphyletic stems from Herbert Spencer’s principle of the “instability of the homogeneous”—the basis of the so-called biology’s first law (McShea and Brandon 2010; Brandon and McShea 2020), and also the second law of thermodynamics as applied to collectives—the random

movement of individuals in space from different groups results in progressive mixing (increase in disorder of configurations). The unmixing requires a directional effort (e.g., spatial sorting of some sort [Shine et al. 2011]). It should be noted that Bretskyan units can be composed of monophyletic units, but this requires very specific mechanisms of aggregation, such as formation of kin groups such as human families (but see Rosenberg [2022] for a different view). The Bretskyan units at smaller spatial scales can be highly integrated and thus described as holobionts or even holobiont-derived organisms in a strict sense (such as eukaryotes). The Bretskyan units, which form at larger scales and are composed of thousands to millions of species, are separated from other such units by externally forced isolation by means of geographic barriers. The large-scale Bretskyan units can be subunits of still larger units up to the ultimate scale of the largest geobiomic unit that also has a phylogenetic significance—Gaia herself. To reiterate, here the term “Gaia” is used as the given name for the largest Bretskyan unit on our planet, which is characterized by both ecosystem and genealogical properties.

Geobiomes have one significant difference from holobionts, in that their biotic parts are usually sparsely dispersed in the abiotic environment and a significant number of interactions at all scales is dominated by interactions with that physical environment. Therefore, the physical environment is at the same time the embedding matrix for a geobiome and a causal constituent part of it. Geobiomes are principal geobiological individuals. At larger scales, they have a potential to change physical conditions to a significant degree and thus are self-modifying vectors of their own evolution (Kiessling 2009; Knoll and Nowak 2017)—they, to a significant degree, are causes and effects of their own change.

The central tenet of the Bretskyan hierarchy is the integration of polyphyletic individuals, by means of isolation, which can be sustained by means of biotic interactions or by means of externally enforced formidable physical barriers. The large geological structures of greater size or areal extent, belonging to the geological time scale hierarchy, are longer lasting than smaller geological structures—oceans last longer than seas, which last longer than lakes; and continents last longer than large islands, and large islands last longer than small islands due to works of erosion. While cores of continents last eons—billions of years (Nance 2022), oceanic islands usually last millions to tens of millions of years (Clague and Dalrymple 1987). Similarly, ocean basins, which are larger than epicontinental seas by orders of magnitude, last tens of millions to hundreds of millions of years (Björck 1995; Woodcock 2004). This is a hierarchy of sizes and, therefore, significance of effects. Also, smaller structures are parts of larger structures, and therefore represent a case of compositional scalar hierarchy (smaller things inside larger things). For example, a pond could be a part of a terrestrial valley, which is a part of a plateau. A pond exists for a shorter period of time than a valley, which exists for a shorter period of time than a plateau. The geographic area and the duration of Bretskyan units are therefore congruently determined by scaling of sizes and durations of geological/geomorphic structures. The phylogenetic congruence of biota inside Bretskyan units can be measured by proportion (and ranks) of endemic taxa. At the scale of the planet, the entire clade “Earth’s life” becomes spatially located, and therefore is equal to the largest Bretskyan individual (Fig. 1). At the singularity of the largest scale, contiguous assemblage of all taxa becomes completely monophyletic.

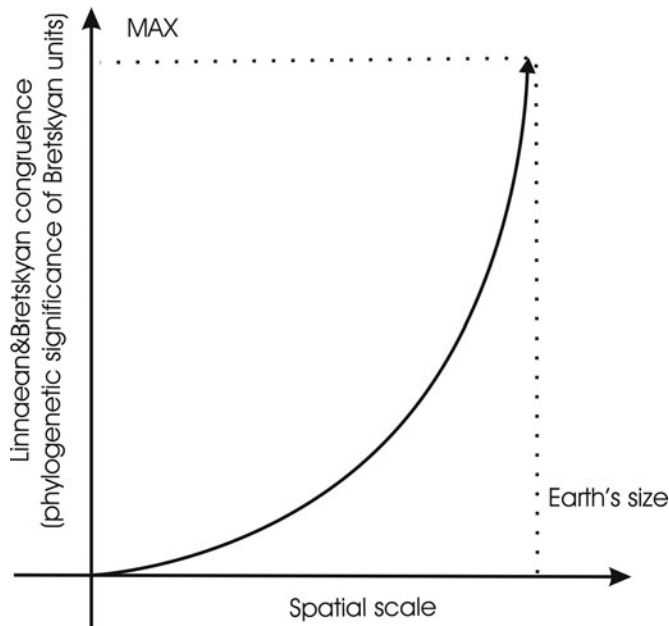


Figure 1. The congruence of the Bretskyan hierarchy of geobiomes with the Linnaean hierarchy of taxa and clades. At the smallest scales, random mixing dominates and the significance and duration of physical barriers of dispersal of organisms are low. The probability of encountering barriers and the duration of these barriers increases as a function of scale—larger physical structures have a higher chance of persistence. Isolated islands, lakes, epeiric seas, or whole continents will impose multimillion year congruence in phylogenies of clades that occupy these areas. The larger the Bretskyan units are, the longer their probable persistence time and the higher their phylogenetic significance. At the largest scale of the planet, the Bretskyan and Linnaean hierarchies converge into singularity of the largest clade and the largest geobiome—Gaia. Because taxa at high taxonomic levels are spatially well mixed on our planet at smaller scales, when we approach the size of the whole planet, the congruence of Bretskyan units and Linnaean taxa should rise sharply, thus forming a concave upward relationship.

Geological time scales are constructed by recognizing the hierarchy of significance of events subdividing Earth's history into time intervals typified by unique features. These geochronological subdivisions have their stratigraphic equivalents represented as sets of all geological bodies formed at given time intervals, from the largest rank to the smallest: eonothems, erathems, systems, series, and stages (Ogg et al. 2008). Time and structure are intrinsically linked in geology and reflect the hierarchical nature of planetary change. No scientific discipline better reflects this than sequence stratigraphy, which ties patterns of structure to concrete physical events and uses them to recognize hierarchically organized patterns, repeated at many scales, for geological time subdivision and correlation of isolated strata (Catuneanu 2006; Miall 2010). The progress of geological mapping has enabled the restoration of paleogeography (paleotectonic configurations) in 4D, thus recognizing the hierarchical composition, assembly, and disassembly of continents, oceans, and smaller terrains (Torsvik and Cocks 2016).

The topographic barriers caused by compositional differences and physical forces affecting the solid Earth create not only barriers for the dispersal of biota but also compartmentalize geological and other geophysical processes in space as well as time, thus creating a hierarchy of sedimentary basins and regional to local climates. Therefore these $\approx 2D$ features continue for significant periods of time, thus forming branching and merging 3D anastomosing (reticulated treelike) networks of ever-changing geological

structures and processes. The geobiological Bretskyan hierarchy essentially inherits this structure. Currently, the closest approach that tackles such structures is so-called macrostratigraphy, which quantifies gap-bound or hiatus-bound sedimentary “packages”—archives of relatively homogenous paleogeographies at sub-continental scales (Meyers and Peters 2011). This information can be used in studying spatiotemporal changes in Earth systems (Peters et al. 2022). Lithosomes—geological formations, or even higher-order lithologically defined bodies such as groups or supergroups (Murphy and Salvador 1999), which represent time intervals of tens to hundreds of millions of years at still larger spatial scales—are the archives of compartments of Bretskyan units that preserve information on physical conditions and sizes of geobiomes.

Longer-lasting geobiomes experience more rounds of microevolution and macroevolution. The exact shape of the spatial scaling relation between the geographic sizes/areas of Bretskyan units and the coherence between Bretskyan units and Linnaean taxonomy will depend on the geophysical state of dynamics of the planet. For example, if the plate tectonics is intermittent with the “single lid” tectonics regime (as appears to be the case [Stern 2023]), then we should expect extreme differences in levels of geobiomic individuality and consequently rates and patterns of coevolution between the Mesoproterozoic and Neoproterozoic–Phanerozoic eons.

This view of connection between spatial and temporal scales resonates well with the “sloshing bucket” model of evolution (Eldredge 1999, 2003), wherein large-scale changes in taxonomic composition and ecological functioning need proportionally larger external perturbations (Fig. 2). Large-scale perturbations are either rare and their recurrence time is long (Raup and Sepkoski 1982, 1984; Lieberman and Melott 2007) or of long duration (Lovejoy 2015; Spiridonov and Lovejoy 2022).

The Bretskyan hierarchy of holobionts and geobiomes connects in the conceptual understanding of the major transitions in individuality (Buss 1987; Maynard Smith and Szathmáry 1998) with the existence of biological hierarchies (Eldredge 1996; Tëmkin and Eldredge 2015). In the presented view, borrowing David Queller's terminology (Queller 2000), the “egalitarian” major transitions (integration of polyphyletic communities into higher-level individuals) as opposed to the “fraternal transitions” of genetically related individuals in forming higher-level integrated evolutionary entities can be understood as self-isolation and self-integration processes working in the lower tiers of the Bretskyan hierarchy. Because the most species-rich clade of life, the eukaryotes, are a result of one such historical individuation event, we can posit that Bretskyan and Linnaean kinds of hierarchies can be nontrivially connected and supply individuals in both directions in a rank-free way (Bretskyan units \rightleftharpoons Linnaean units). When we are describing Bretskyan and Linnaean *kinds of hierarchies*, we mean that the same logic of subdivision into ancestry-based treelike patterns (Linnaean kind) and spatially and temporally isolated and coevolution and/or physical isolation-bound patterns (Bretskyan kind) can also be applied to other evolving systems: for example, cornets could be seen (Tëmkin and Eldredge 2007) as units of cultural evolution forming phylogenies, but they also can be seen as being parts of semi-isolated temporal and spatial evolving cultural units having both economic and genealogical components (Bretskyan-like hierarchy or “maker hierarchy” in the cultural realm [Eldredge 2009]). If viruses are a grade of organization—self-replicating coalitions of sequences that appeared many times by means of individuation

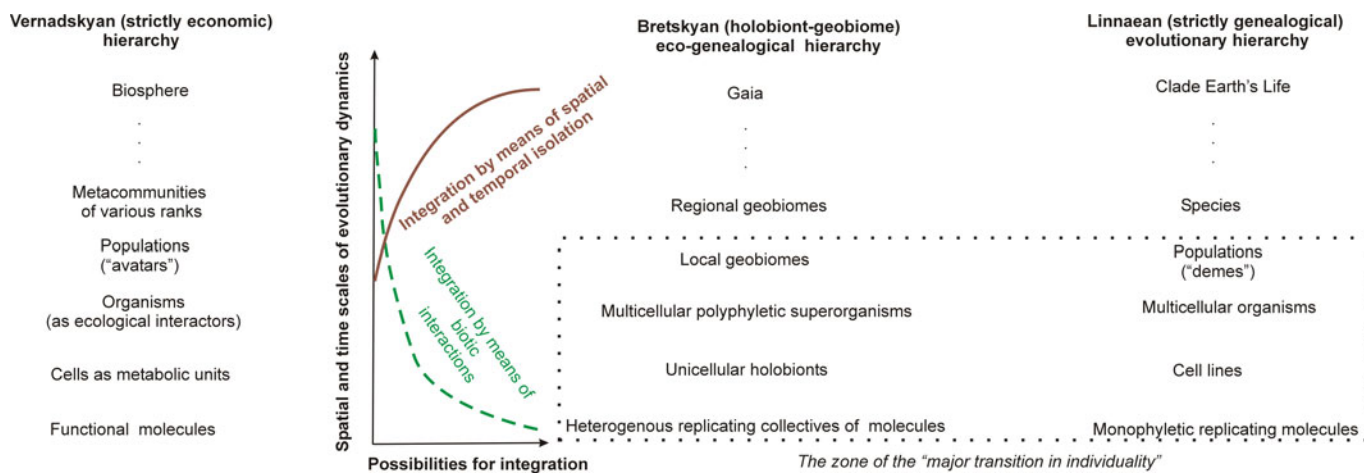


Figure 2. Conceptual diagram that frames the relations between the economic hierarchy of functional communities, the Linnaean hierarchy of clades, and the Bretskyan hierarchy of holobionts and geiobiomes. Community units have high chances for evolutionary integration into discrete individual-like modules at the very smallest and at the largest scales. At the smallest scales, the unity and integration is achieved by means of cooperation or other forms of symbiosis between limited numbers of individuals at that level. The dotted line shows the zone where classical “major transitions in individuality” are probable: (1) egalitarian in the Bretskyan hierarchy and (2) fraternal in the Linnaean hierarchy. As systems become larger, the number of components (interacting species) grows, as does the variance in their traits, which makes integration of polyphyletic and polymorphic individuals harder and harder. Then, at still larger spatial and temporal scales, another and unrelated factor starts to play the prominent role in integration of polyphyletic ecological communities into evolutionary units—the force external to the biota itself—spatial isolation, that is, geology in a broad sense. Because the size of spatial barriers is directly related to their durations, this means larger and more diverse ecological entities are more likely to be isolated for longer periods of time from any such similarly sized (hierarchically comparable) entities. At larger sizes of geiobiomes, effective integrating coevolution will be more and more visible if we compare biogeographic units of increasing size. The changes in such units can be apparent, due to their size inertia, either through a long time or by means of rare but exceedingly powerful events—the “sloshing bucket” mechanism of larger entities needing larger/longer perturbation for initiating evolutionary change (Eldredge 1999, 2003). As in the case of water level in the metaphorical “bucket,” we need sufficiently large in magnitude perturbation in order to permanently change the volume of the liquid or, in the case of geiobiomic evolution, the composition of biota in a province.

from more complex cellular ancestors or their plasmids (as was inferred by [Kazlauskas et al. 2019])—each separate independently originating monophyletic branch of “virus-level” evolutionary units could be understood as a separate hierarchy of the Linnaean kind.

The dual hierarchy view (first introduced by Eldredge and Salthe [1984]) accentuates the distinction of germ and soma (the Weismann barrier) or “functional” and “reproductive” in biological hierarchies. There is basic ontological truth to this generalization. On the other hand, the specialization of cells in organisms to function as reproducers of organisms or as servers of the organism’s current function (with similar specializations at lower levels of cells and higher levels of superorganisms or eusocial colonies) is an evolved feature of subdivision of labor (Simpson 2011). Here, using the population genetics definition of fitness as a relative contribution of a given type to the next generation (or “probability of reproductive success”), we can think of somatic cells (non-reproducing individuals at the cellular level) as cells having zero long-term fitness ($w \approx 0$), and germ cells as having larger than zero fitness ($w > 0$); therefore, we can think about them as heterogenous dimorphic populations with respect to fitness. The same principle applies to animal superorganisms, such as eusocial hymenopterans. On the other hand, somatic cells, as well as workers in hymenopteran colonies (Bourke 2011), have a potential to “darwinize back” (using the terminology of Godfrey-Smith [2009])—in the first case, cancers emerge, in the second case, disintegration of the colony through parasitism (which is dynamically equivalent to cancer) ensues, workers in a sense become parasites of their own colony. Darwinization is understood here (following Godfrey-Smith [2009]) as reacquisition of autonomy in reproduction of individuals at a given level, and the transition from epigenetic reproduction control (Simpson 2011), which is dependent on organismal (as in the

case of cells) or colony-wise (as in the case of superorganisms) context, to genetically controlled reproduction; in other words, there is a reacquisition of capacity to participate in dynamics driven by mutation, selection, and statistical drift. We should emphasize that the same conceptualization can be repeated at many levels of economic, genealogical, and Bretskyan hierarchies: eukaryotic cells can be conceptualized as economic powerhouses, as coevolving heterogenous/polyphyletic collectives, or as single replicating units, as can organisms (unicellular and multicellular), colonies, and so on. The fluidity in exact definition and fuzziness of boundaries of the paradigmatic individuals—the organisms—which is very apparent in plants (White 1979) or fungi (Lakovic and Rillig 2022), strengthens the case that in principle, we can treat most spatially and temporally contiguous (if not all?) biological entities as Bretskyan units of differing inclusivity levels. Consequently, we can conceptualize cases of emergence of cancers and their competitive dynamics with native cells inside organisms as also being of the Bretskyan unit type. There have been numerous attempts at understanding the sub-microevolutionary dynamics of cancers in ecological paradigms (Walther et al. 2015; DeGregori and Eldredge 2020)—coevolution of spontaneously evolved (darwinized) unicellular parasites usually results in the death of an organismic Bretskyan unit. But sometimes a given cancer becomes successful and evolves into a transmissible form (Murchison et al. 2010) or acquires a completely new niche (Van Valen and Maiorana 1991), while in other cases, neoplasm cells become able to “steal” organelles from their hosts (Rebbeck et al. 2011)—the inside-community large-scale gene transfer resulting in long-term survival of a parasite by means of escaping the boundaries of its ancestral multicellular organism.

A major difference between the Linnaean and the Vernadskyan hierarchies is the problem of formulating

heritability in ecosystems. For evolution to happen, the progeny should resemble the parents (Lewontin 1970), or more generally there should be significant temporal correlation between the states. Ecosystems are constituted of two components—the living populations, which are characterized by genetic heritability, and the nonliving one, which is harder to conceptualize with respect to heritability. Here we argue that both of these components have heritability, and the heritability of a nonliving system is well recognized in the geological time scale hierarchy—geologists routinely trace fission and the coalescence of continents and terrains at all time scales (Table 1). What enables the determination of this geodynamic phylogeny of geological bodies? The essence of heritability is the inertia or tendency for persistence—it can be achieved by a number of ways. In biology, the key role is played by replication and the adaptive error correction. In geology, persistence emerges in a number of forms, for example, (1) mechanical/thermal/chemical durability, such as in the case of zircons, which can persist as components of rock for eons; (2) dynamic stability enabled by buoyancy, such as in the case of low subduction potential of continental crust, which also has potential for indefinite persistence; (3) and the size itself—due to locality of interactions, larger structures are harder to modify (e.g., by erosion, which works on surfaces). All these factors determine time scales of persistence and therefore heritability of geological features. Persistence-based natural selection is apparently a universal feature across all kinds of systems (Lieberman and Melott 2013). The persistence of geological structures causes the persistence of both living and nonliving components of ecosystems while explaining the nonliving matter part of the ecosystem heritability equation. Therefore Bretskyan units are characterized by two equally important kinds of heritability: (1) replication of genealogical units of all ranks and (2) geologically caused persistence of the physical space and material properties of matter they occupy and are immersed in.

We should mention that in the original definition of the dual biological hierarchy theory (Eldredge and Salthe 1984; Eldredge 1985, 1986), organisms were considered to belong to both genealogical and economic hierarchies, thus being the crucial connection between functional and genetic multilevel processes. In this sense, by recognizing the special status of the organism level, the dual hierarchy approach already suggested the need for the intermediary hierarchy of eco-genealogical entities. Our present work reveals that the ecosystemic interactions and genealogical significance to varying degrees can be found in many spatially and temporally bounded biological structures. The Bretskyan hierarchy simply explicitly acknowledges all these properties and frames their relative significance in biological ontology as a function of size and duration of the studied entities located in real space, time, and material matrix (Table 1).

Hierarchy of Physical Barriers, Forced Individuality of Large-Scale Bretskyan Units, the Concept of Multiscale Allopatry, and the Kinds of Bretskyan Units

Isolating mechanisms are enablers of the emergence of individuality of higher-level evolutionary units: speciation is a paradigmatic case in which populations split due to internal incompatibilities or due to external barriers that prevent gene flow, which can result in quick extirpation of incipient species (Allmon et al. 1998; Stanley 2008), or alternatively in often punctuated change and subsequent stasis of a lineage (Stanley 1979; Futuyma 1987; Eldredge et al. 2005; Hunt 2007). Another

important set of aspects includes spatial structures of populations and locality of their interactions (Dieckmann et al. 2000) and the multiscale heterogeneity of environments (Jablonski 2008a). For example, even in the earliest stages of evolution before the emergence of cells, the locality of self-replicating chemical reactions on 2D surfaces should have significantly contributed to the emergence of organism-like reproducers (Szathmáry and Smith 1997; Czárán and Szathmáry 2000; Szathmáry 2015). The spatial separation itself can be understood as a form of quantitative/graded isolation—the interactions are exponentially more plausible in proximity than with distance (Edelstein-Keshet 2005). Spatial separation individuates the constituent populations of a species, while forming clinal variation (Gould and Johnston 1972; Yablokov 1986) and complex spatiotemporal patterns of microevolution (Lieberman et al. 1995; Brombacher et al. 2023).

Even though the raw separation in space is an important factor in isolation, life-forms evolved and were subjected to a range of more effective isolating mechanisms that played a role in generating and sustaining evolutionary individuality. The acquisition of cellular structures of autonomous life-forms—the lipid membrane, separating the internal molecular network from most of the external genetic material and metabolically active molecules, was a key step in organizing replicating molecules into cooperative evolutionary units (Maynard Smith and Szathmáry 1998). The recognition of members of your own colony is an essential integrating mechanism in maintaining superorganismal individuality (Wilson and Hölldobler 2005; Nowak et al. 2010). The strongest cases of in-group and out-group recognition can be found in the most integrated individuals—for example, the CRISPR-Cas immune system in archaea and bacteria at the single-cell level, defending the cell from foreign genetic parasites/influences (Koonin and Makarova 2019), and the more familiar but far more complex immunity and cell recognition mechanisms inside multicellular organisms (Gilbert and Tauber 2016). Also in the paradigmatic cases of individuality at the species level, active reproductive isolating mechanisms are crucial in maintaining individuality of species by means of Paterson's "species mate recognition system" (SMRS; Vrba 1980; Vrba and Eldredge 1984; Paterson 1985).

Allopatric speciation and its para- and peripatric variations (Gavrilets 2004)—a kind of speciation due to geographic separation of ranges—is thought to be the major factor responsible for the individuation of populations and, consequently, generation of new species (Dobzhansky 1937, 1940; Mayr 1940; Eldredge 1971; Eldredge and Gould 1972; Allmon and Sampson 2016; Hernández-Hernández et al. 2021; Anderson and Weir 2022). There is a growing amount of evidence that the Earth's geomorphic structures play the major role in generating biodiversity (Rahbek et al. 2019), following the idea that the complexity of the planet is the main modulator of diversity and stability of habitats (Archibald et al. 2010) and isolation opportunities (Cracraft 1982). Therefore, speciation and extinction processes are intrinsically linked to the structure and dynamics of the Earth and its climate (Stanley 1990; Vrba 1993). The same recurring principle of environmental heterogeneity in maintaining and generating diversity apparently scales down to even short-term ecological processes, which helps to explain the so-called Hutchinson's paradox of the plankton (Hutchinson 1961; Descamps-Julien and Gonzalez 2005). If the system is scaling and multifractal, such as topography or the geology of the planet (Gagnon et al. 2006), then we should expect non-uniformity (much more extreme than Gaussian) at all spatial and temporal scales—for

example, some regions can be topographically very rough, while others have very low relative variability in any of the measured parameters, therefore creating very quickly changing biomes, as in mountain ranges, or the opposite, the very monotonic features such as the Great Eurasian Steppe or the Amazon rain forest. And even here heterogeneity plays a role, such that the former biome is desolate and species-poor, while the latter is species-rich. The complexity in macroevolution is usually meant as a single-level quantity—a scalar—although it is (in the case of scaling systems such as Earth) a multiscale property, which can be represented by a spectrum or structure function of the scale. Here we use the definition in a latter meaning—the Earth is heterogeneous and diverse at multiple resolutions.

Speciation and extinction dynamics exhibit significant coherence between clades—X-genealogical turnovers—at both the regional (Vrba 1985, 1992) and global scales (Sepkoski 1981, 1984; Bambach 2006; Alroy 2010; Cuthill et al. 2020). This pattern signals the importance of common external drivers of biodiversity dynamics usually tied to changes in climate states, sea level, extra-terrestrial causes, and tectonics (Valentine and Moores 1970; Alvarez et al. 1980; Finnegan et al. 2012; Stigall et al. 2019; Mathes et al. 2021; Spiridonov and Lovejoy 2022). Some of the best examples relevant for the establishment of the picture of hierarchical emergence and persistence of geobiomes come from studies of Paleozoic marine faunas or of so-called coordinated stasis of multiple lineages and community patterns (Brett and Baird 1995; Brett et al. 1996). The majority of lineages formed recurring communities, and the taxonomic and ecological turnover was concentrated within relatively short periods of time (Ivany et al. 2009). The application of dynamical systems tools to Silurian Period faunas revealed that the patterns of species dominance were modulated by oceanic circulation and sea-level states and sharp transitions between them (Spiridonov et al. 2015, 2016, 2017a,b, 2020b; Venckutė-Aleksienė et al. 2016; Spiridonov 2017; Crampton et al. 2018; Whittingham et al. 2020), with a pattern showing coherence in space (Spiridonov et al. 2020a) and repeating itself at several time scales (Rinkevičiūtė et al. 2022). The spatial evolutionary processes are modulated by sea-level change, climate, and tectonic perturbations—these factors play a crucial role in modulating diversity at large temporal and spatial scales (Lieberman and Eldredge 1996; Lieberman 2003; Radzevičius et al. 2016; Stigall et al. 2017).

From such paleobiogeographic and macroevolutionary examples discussed earlier, we implicitly can see the hints of a general pattern suggesting what we call hierarchical or multilevel allopatry, which should be directly related to the nature of geophysical processes and the hierarchical structure of the planet. The classical examples of coordinated stasis and species factories show the importance of sea-level and climate perturbations, which generate repeated episodes of isolation (= individuation of species and whole local geobiomes) and dispersal of newly generated taxa (Stigall et al. 2017). Epeiric seas are shallow and thus susceptible to relatively small-magnitude sea-level/climate changes. Such changes could be generated by relatively fast “grand” Milankovitch cycles with period lengths of 1.3–2.6 Myr (Van Dam et al. 2006; Crampton et al. 2018), and possibly by even faster precession cycles at scales ≤ 25 kyr (Crampton et al. 2020). These time scales of millions of years are commensurable with durations of separate species and do not allow a deep repeated multigenerational (measuring in species generations) coevolution. Therefore, the scale of species-level multigenerational coevolution should correspond to the continental or oceanic spatial scales and the

time scales of tens of millions of years. The concept of a continent and its distinction from an island is an arbitrary one. The same goes for oceans and seas. Tectonic plates exhibit power law scaling or a “scale-free” pattern, which means plates do not have characteristic sizes (Sornette and Pisarenko 2003). The same applies to the fragmentation index of continents—meaning that we should expect fragmentation to happen on all time scales (Spiridonov et al. 2022). Due to positive scaling of fragmentation indices with increasing time scales, we find the largest differences between continental configurations at the longest time scales. Therefore, larger spatial structures on average have more formidable barriers, which also in turn last proportionately longer. The connection of large geographic sizes and long durations, which are far longer than typical species durations (typically of millions of years [Raup 1991; Cooper and Sadler 2010; Žliobaitė and Fortelius 2022]), implies the significance of these planetary structures in keeping forced individuality of geobiomes (Fig. 3).

Bretsky units at larger scales—although more fuzzy than, for example, species, which also have a property of fuzzy/non-sharply separated sets (Van Valen 1978)—are true ontological individuals, because they are spatiotemporally bounded, with origins, historical durations, and terminations. The apparent fuzziness of geobiomes stems in part from our scale-boundedness as observers. There is a growing appreciation of such geobiomic ontology (Ung and Buttigieg 2023). Geobiomic units constitute a rank-free scalar hierarchy in space and a network-like structure in time. As seen in time, the Bretsky hierarchy resembles a braided river with anastomosing units emerging, merging together, separating, or changing hierarchical significance in space depending on the degree of isolation as barrier intensity and spatial extent fluctuates (Fig. 4). This flow of geobiomic individuals at long time scales achieves global mixing, when all previously separated units (through contacts with neighbors) exchange/percolate evolved biotas. It was estimated that these mixing or synchronizing processes led by plate tectonics, such as “Noah’s Ark”/“docking events” of continents or islands (McKenna 1972), start to dominate diverging local and regional tendencies at time scales longer than 40 Myr (Spiridonov and Lovejoy 2022, 2023). Such mixing events, which work in synchronizing and homogenizing biota at long time scales, are now well documented. One example is the connection event where trilobites of genera *Kootenia* and *Bailiella* from the previously distinct western Newfoundland “Pacific Province” and eastern Newfoundland “Atlantic Province” were found together showing the merger event and the origin of a new larger fused Bretsky paleobiogeographic unit during the middle Cambrian (Kay and Eldredge 1968). The great American biotic interchange (GABI) is another great example (Marshall et al. 1982) that will be discussed later in the paper.

Larger and more formidable geological structures serve as barriers for dispersal of biota for longer periods of time. Thus, we should expect a hierarchy of coevolutionary processes in space and time that integrates geobiomes into hierarchical symbiotic collectives—larger geobiomes with more formidable dispersal barriers will experience proportionately more integration with more constituent taxa (Fig. 5). It shows allopatry as a scale-free concept—the same repeating principles of isolation and contingent divergence are applicable not only at the species level but also for much larger and far more complex entities. The dynamics of geobiomes, though, have a significant difference with allopatric speciation, because Bretsky unit isolation is inevitably followed by coalescence (yet hybridization between closely related sister

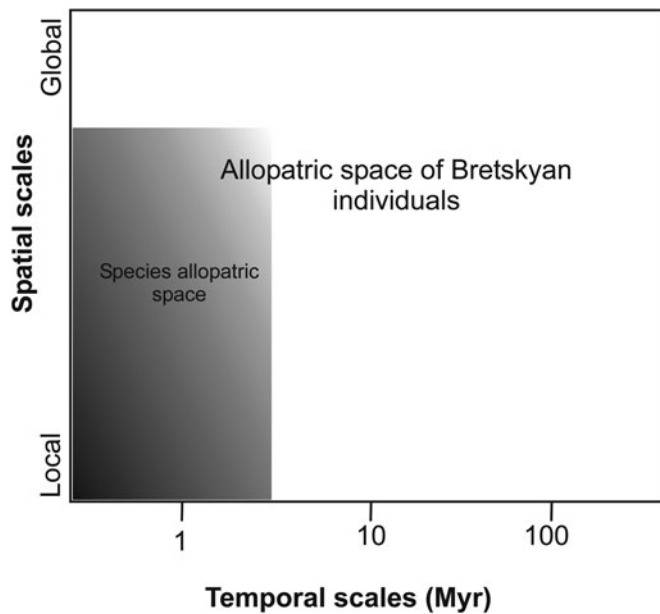


Figure 3. Allopatric space and the hierarchies of allopatries. Species-level allopatry requires relatively short time scales—higher end estimated from the duration of species, which is on the order of several millions of years, although it can potentially occur in a large space, depending on the dispersal abilities of taxa. Here the species allopatric space is a subset of Bretskyan units' allopatric space—where whole biotas (“provinces”) diverge and experience coherent coevolution and integration in externally isolated or semi-isolated ecosystem units. The size of a province need not have a particular scale and can be a fragment of a biota of any size larger than a certain threshold determined by the characteristics of the planet’s geodynamics, which determines the intensity, duration, and other physical parameters crucial for biotic isolation and persistence of the isolation for a sufficient amount of time.

taxa is not at all uncommon). In this way, the dynamics of Bretskyan units or geobiomes topologically can be described as representing a process akin to hierarchical “sexual reproduction.” This concept perhaps sounds rather exotic, but it can be described in a clear way—in a multilevel process of fragmentation and merging of geobiomes, smaller geobiomes diverge and merge with other smaller geobiomes, thus sharing evolved features and coevolved relations with each other at short time scales; while at the same time these collectives of isolating and coalescing geobiomes constitute still larger geobiomes that repeat the process at still longer time scales and larger space scales, and so to infinitum or in the real world to the limit of the size of a planet with active geodynamics. Here individuality of geobiomes emerges and disappears in a scaling manner: there is a continuum and proportionality of their sizes and durations. The structures on our planet are characterized by multifractal variability (Spiridonov et al. 2022), that is, they are scaling, self-similar, and show strong variability at all scales.*

*The key in understanding hierarchy of sizes and durations of geobiomes is so-called multifractal theory, which models processes as representing hierarchical cascading multiplicative interactions of geological and geophysical variables. Multifractal models imply concentration of variability at the smallest scales and show striking unevenness at all scales where scaling regime is applicable. Multifractal structure in its essence represents a field where each point is defined by a value in opposition to a fractal set to which the element could belong to or not. Multifractals are characterized by self-similarity at all scales, while each value of intensity of a variable (e.g., topographic height) is defined by its own fractal exponents—therefore, multifractals are characterized by an infinite hierarchy of such exponents (Schertzer et al. 2010). One of the approaches that can be used in

A similar observation was made by Charles Darwin almost 200 years ago, when he, during the voyage on the *Beagle*, compared floras of two sides of the Andean mountains (Darwin 1839: p. 399): “I was very much struck with the marked difference between the vegetation of these eastern valleys and that of the opposite side: yet the climate, as well as the kind of soil, is nearly identical, and the difference of longitude very trifling.” Later he continues, implicitly linking the contrasts in floras and faunas to the great size, height, and consequently long duration of the Andes, which he understood as an epochal barrier: “This fact is in perfect accordance with the geological history of the Andes; for these mountains have existed as a great barrier, since a period so remote that whole races of animals must subsequently have perished from the face of the earth.” Although the concept of scaling did not exist when Darwin wrote these words, the implicit link between the dimensions of geological structures and their geological longevity, and as a consequence their significance in producing biological diversity, was hinted at in these earliest observations of modern science.

Barriers to the spread of holobionts exist not only in geography, but also in time—sharp environmental changes of short duration and large magnitude cause the demise and consequent turnover of the global biota (Raup and Sepkoski 1982; Bambach 2006). Similarly, as in the case of topography, mass extinctions, and presumably their causes, are the extreme right tails of continuous distributions (Marshall 2023). The majority of extinctions and originations at the global scale are probably caused by many such impulse-like perturbations of varying sizes (Foote 2005). And indeed the statistics of global originations and extinctions at scales of millions of years and also populational processes at shorter time scales of tens of thousands of years show the signature of multiplicative multifractal variability (Plotnick and Sepkoski 2001; Yacobucci 2005; Spiridonov et al. 2016; Spiridonov and Lovejoy 2022), which implies sharp, intermittent (typified by extremes), and hierarchically modulated changes in time that, as seen from the Bretskyan units perspective, create sharp temporal boundaries in the composition of the biota (up to time scales of tens of thousands of years [Crampton et al. 2020]). These findings support the idea that the global biota—Gaia—experiences and transitions through sharp separation events from its previous compositional states. The marine animal “communities” originally studied and distinguished at time scales of geological periods (tens of millions of years) by Bretsky (1968) were essentially representations of Gaia. The geological time scale, which is itself hierarchical, reflects the levels of severity of the

reducing this potentially infinite complexity is so-called universal multifractal formalism, which describes the extreme behavior using a low number of parameters (Lovejoy and Schertzer 2013). Topography, geology, and climate of the Earth are apparently best described by multifractal (scale-free) structuring (Gagnon et al. 2006; Lovejoy 2018), which shows scaling, wide range, and hierarchically organized stochastic variability spanning many orders of magnitude. Because biota inherits this geophysical variability, we should expect similar, in-kind, extreme variability and unevenness in the degree of isolation, size, and duration of geobiomes. Therefore, we should expect a wide range of variability in degree of geobiome individuality or mutual separateness, evolutionary and ecological disparity between geobiomes. We should expect unevenness and diversity of all characteristics at all space and time scales. Because sizes and durations of geobiomes are connected, larger sized, and of long duration, geobiomes should be rare, but much more common than if they had been characterized by Gaussian variability. Moreover, multifractal variability, which implies stochastic hierarchical multiplicative structuring of spatial geological features, is also typical for geological structures of other rocky planets (Landais et al. 2019). Therefore, the described theory should be applicable for other habitable worlds if such were found. For deeper understanding of multifractals and scaling in geosciences, the reader is directed to a dedicated work by Lovejoy and Schertzer (2013).

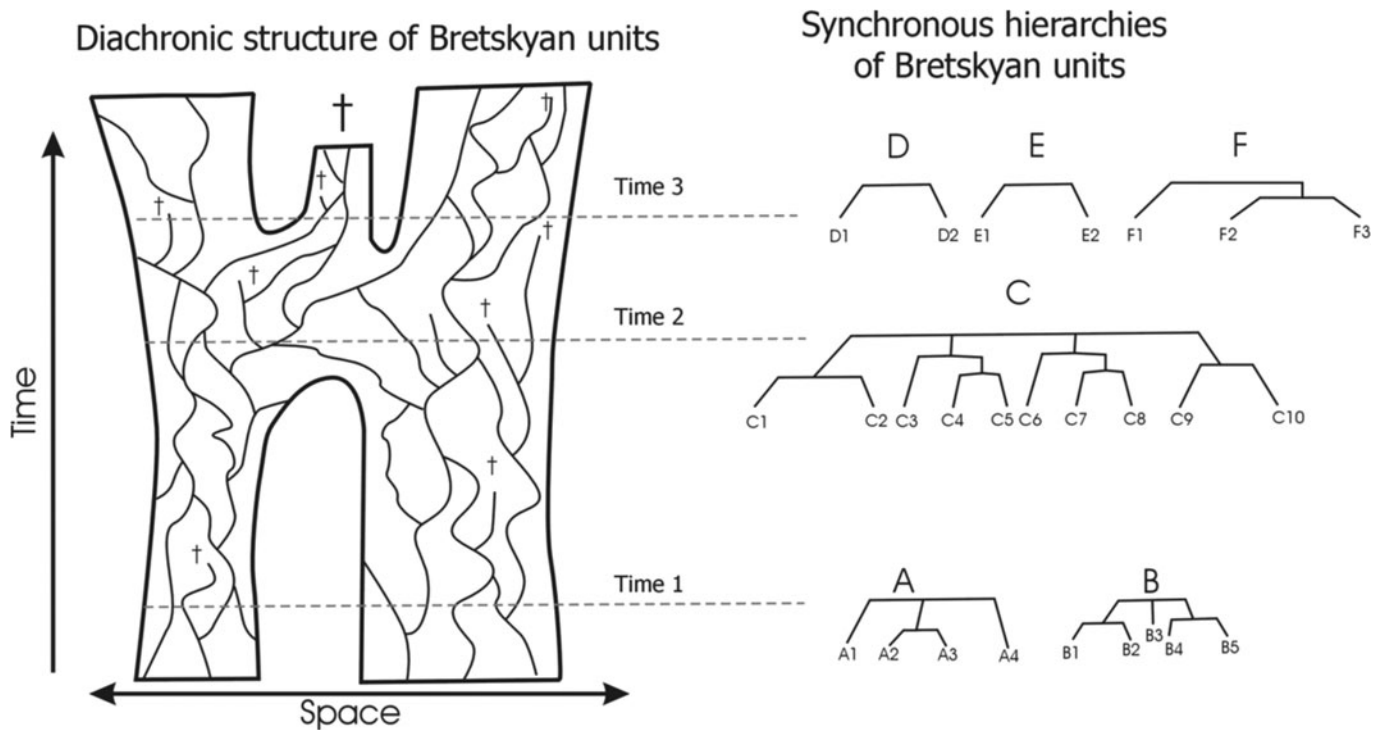


Figure 4. Conceptual figure of spatiotemporal dynamics of large Bretskyan units (geobiomes) at two levels. On the left side of the figure at Time 1, we start with two large-scale geobiomes (bioprovinces) that are also composed of many smaller persisting, splitting, fusing, and disappearing geobiomes. At Time 2, we have a merger event of two provinces that become one. At Time 3, we have the fission of province C into three new provinces D, E, and F. During this time period, province E goes extinct (e.g., during disappearance of an isolated oceanic basin during collision of continents). On the right-hand side of the figure, we can see the strict (although fuzzy to different levels) scalar hierarchical structure of bioprovinces at any given time. Nested patterns show biotic similarities between bioprovinces.

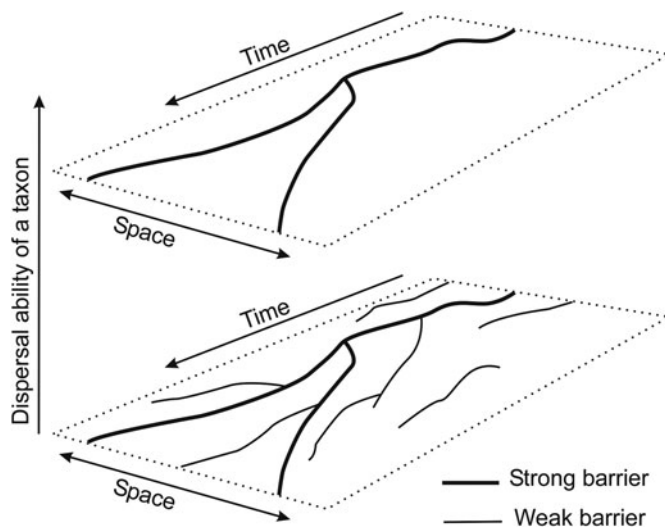


Figure 5. Spatiotemporal evolution of isolating barriers, for the ease of understanding presented in 1D space (x-axis) and 1D time (y-axis), as a function of dispersal abilities of clades (z-axis). Weak barriers have shorter duration and spatial extent (due to positive scaling of durations of geological bodies/barriers in relation to their size). Smaller barriers are sufficiently long-lasting to work as species-generating barriers (species-level allopatric barriers), and larger and longer-lasting barriers work as barriers for large geobiomes (larger-scale Bretskyan units). These very significant barriers (e.g., oceans for terrestrial non-volant species) isolate in tandem many different clades into integrative units. Note that many generations of lower-level barriers (= many generations of species) are present; this makes micro- and macroevolutionary coadaptation all the more likely for the whole biota.

perturbations, or the degree of transformativeness more generally, in the evolution of Gaia.

It was suggested that, although of a very different nature, mass extinctions represent a kind of “major transition in evolution” (Currie 2019) similar in importance to traditional “major transitions” instances of purely creative eukaryogenesis or the origins of the human language (Maynard Smith and Szathmáry 1998; Bickerton 2009; Calcott and Sterelny 2011). In the light of the presented theory, mass extinctions indeed could quite literally be seen as the major transitions in evolutionary individuality between compositionally and functionally differing states of Gaia. These temporal barriers are, of course, different from spatial barriers due to the presence of “time’s arrow” or the irreversibility of the time dimension, although similar in other aspects. As biotas can be starkly distinct on continents isolated by strong environmental barriers in space, similarly biotas can be starkly distinct by means of their sharp environmental isolation in time—they differ in ecological functioning (Wagner et al. 2006; Aberhan and Kiessling 2015) and the states of macroevolutionary dynamics (Miller and Foote 2003; Jablonski 2005; Brayard et al. 2009; Alroy 2010), including in geographic space itself (Krug et al. 2009). Therefore, Gaia (i.e., differing instantiations of Gaia in different times) as the largest units in the Bretskyan hierarchy, separated by mass extinctions, show significant structural and functional differences and thus can be seen as sequential individuals with ancestor–descendant relations occupying approximately the same space. The same arguments work for mass originations and

mixtures of high rate of extinction and origination events (Marshall 2006; Cuthill et al. 2020).

In a similar vein, the International Chronostratigraphic Chart represents a hierarchy of changes in the composition and functioning of global Bretskyan units; regional and local stratigraphic scales, especially when based on biostratigraphy, should to a significant extent represent transitions in states of smaller in areal extent, regional and subregional Bretskyan units. Therefore, geological time scales reflect ontologies of change in individuality of geobiomes. One such example is the NALMA (North American land mammal ages) time scale subdividing Late Cretaceous to Cenozoic terrestrial sequences of North America based on the compositional changes in mammalian assemblages at the continental scale (Flynn et al. 1984). The apparent diachrony of

first and last appearance events in different regions of North America (Alroy 1998b) can be understood as a reflection of the presence of finer-scale geobiomic substructures in the North American geobiome.

We can conceptualize some important evolutionary events as representing additional major transitions of individuality—the major transitions in kinds of sub-Gaian Bretskyan units—examples of which are terrestrialization and the expansion of life into the open ocean or Earth's deep interior (some of the “megatrajectories” of Knoll and Bambach [2000]). For example, terrestrialization at the beginning of the Phanerozoic led to formation of a “parallel biogeography” weakly interacting with its marine geobiomic ancestor (interactions inside the realm are much more important than those outside it). The new characteristics of previously unoccupied environments impose new sets of physical and geochemical constraints and feedbacks on these constraints (Kenrick et al. 2012; Lenton et al. 2016). Such transitions result in qualitatively different drivers, rates, and scales for the coevolution inside Bretskyan units of new type due to radically different ranges of physical parameters of occupied environment. The largest difference between the marine biosphere and the terrestrial one is the topology—the marine biosphere at first approximation is always contiguous. It topologically resembles a plane with holes. On the other hand, continents are essentially islands isolated by hardly penetrable marine barriers. In the future, percolation network approaches (e.g., Palamara et al. 2023) will give us a comprehensive understanding of the nature of differences in temporal topological connectivity of oceanic and terrestrial geobiomes at geological time scales. The example of emergence of qualitatively different geobiomes by means of break-through (escape) into qualitatively new environments of a number of clades, and their later ecological integration, shows that there is a qualitative difference in modes of major transitions at different levels of the Bretskyan hierarchy. Traditional (small inclusivity scale) major transitions (e.g., eukaryogenesis) are dominated by the pure fusion of lower-level polyphyletic units, while the largest scale transition and the origins of the quasi-autonomous terrestrial biosphere is a case of fission of an already formed (and eons old) marine sub-Gaian unit, resembling a higher-order “cladogenetic” event. At the same time, it is also an instance of the growth or expansion (Van Valen 1989) and differentiation of Gaia.

Time Scales of Coevolution inside Bretskyan Units, Fitness Landscapes of Geobiomes, and Spatiotemporality of Contingency, Adaptation, and Progress in Macroevolution

Here we present evidence that the structure of a biota is not an epiphenomenon, as it is sometimes presented (Hoffman 1979;

Bambach and Bennington 1996), but an essential ontological feature of biology, necessary for the causal understanding of evolution. The major obstacle in understanding evolution of communities stems from previous lack of a coherent conceptual framework that could explain the mechanisms of individuation of communities at the whole range of time and space scales. The spatially and temporally defined hierarchy of Bretskyan units is the closest representation of the living world we know of. All interactions (metabolic and genealogical) happen in ecosystems, which are separated to varying degrees from other such systems. The mechanisms and the typical magnitudes of separation and thus individuation vary as a function of scale. At larger scale, the barriers individuating biota have a geological (in a broad sense of the word) origin, and their space–time characteristics are determined by geodynamics. Therefore, the knowledge of the statistical time and space scaling characteristics of geological phenomena provides a unified theory on the patterns of individuation, fusion, and scales of coevolution inside and among geobiomes.

The evolution of holobionts at lower spatial and temporal levels of the Bretskyan hierarchy is a well-developed field (e.g., Gilbert and Tauber 2016). Here we concentrate on the much less understood large spatial and long temporal scales—regions, provinces, and Gaia herself—which respectively can last from thousands to up to billions of years. The main concept here is coevolution and, more precisely, the *geobiomic depth of coevolution*, which is directly linked to the physical characteristics of Bretskyan units. The next concept of importance is so-called fitness landscapes of geobiomes—they are analogues of classical fitness or adaptive landscapes (Gavrilets 2004; McGhee 2006). Characters of geobiomes are statistical organismal-level, populational-level, species-level, or functional characteristics of constituent taxa. Fitness is here understood as the probability of survival/proliferation of evolved characteristics at a given geobiomic level.

Coevolution implies the reciprocal/mutual evolutionary causation of change in two or more groups of individuals (Levins and Lewontin 1987; Thompson 2013). The basic prerequisite for the emergence of coevolution is proximity or overlap of ranges of evolutionary individuals in time and space. Speciation, which is the result of splitting and isolation of one lineage into at least two, entails the separation of microevolutionary dynamics inside these lineages. After the split, lineages follow contingent evolutionary paths while having little genetic exchange of newly acquired adaptations and other traits. Isolated lineages start contingently adapting to the surrounding biotic and abiotic environments, including experiencing coevolution inside the lineage itself (Prum 2017). We can add that even simple models of evolution, with contingent separation and isolation events, result in wide exploration of the morphospace (Niklas 2004; Solé 2022). This is an example of the evolutionary “butterfly effect,” a metaphor based on the short story “A Sound of Thunder” written by Ray Bradbury in 1952. This metaphor says that even small differences in initial conditions of evolving lineages can subsequently cause significant divergence in traits or sequences of selective events (Niklas 2004).

The critical role in defining, and making species coherent entities is played by the SMRS (Paterson 1985); species individuality is maintained by the “glue” of coevolution, which includes gene exchange and a mutual selection and other “economic” effects of organisms in a Red Queen evolutionary mode (Van Valen 1973). Therefore, the individuality of species mechanistically is maintained by more intense interaction between organisms of the same group than with other such groups. These interactions

are only possible if the lower-level individuals in question occupy the same geographic space, and if they reside in the same time interval. The same arguments work for more inclusive spatiotemporal eco-genealogical individuals that constitute the Bretskyan hierarchy.

The genome of a population subject to natural selection maximizes so-called Fisher information (about the environment), here understood as an information measure that reflects an unknown (environmental) probability distribution (Frank 2009)—for example, the presence of thick fur reflects cold climate, fat stores reflect unevenness of food supply, and so on. It was suggested that evolution represents a multilevel learning process (Vanchurin et al. 2022); here we show how this learning is organized in the real-world hierarchies. It should be noted that the information maximized within a population of evolutionary individuals in their genomes is only about “effective” factors that contribute to the survival and expansion of lineages. To understand the importance of maximization of Fisher information in evolutionary dynamics of geobiomes, we should remember that the effective environment (space in which the holobiont evolves) is characterized by size and duration. Therefore we should expect scaling in acquired information about the Earth system by any holobiont or geobiome. The distribution, size, and duration of barriers determine the geodiversity. Geobiomes of larger sizes and durations, and occupying more diverse geological settings, are expected to be more “learned.” Because only part of the environment is a physical one, and the other is the biological one (Levins and Lewontin 1987), we should also expect acquisition of more Fisher information about biota in larger areas. This follows from species–area curves (Rosenzweig 1995) and the law of mass action (the number of possible interactions is proportional to diversity). More species means more ecological interactions from which all species could mutually “learn.” In a larger geobiome, there will be greater coevolutionary depth than in smaller, less diverse, and shorter-lived geobiomes. The rates of biological progress—competitiveness level in as wide a range of biotic and abiotic environments as possible—are directly related to hierarchical dynamics of planetary geology in a broad sense.

Physical isolation works as an integrative external force for isolated monophyletic clades, because it causally divorces some members of the clade from others (Fig. 6). The coevolution of species of a single clade inside a large-scale geobiome (e.g., bioprovince) should structurally resemble the “game against a version of yourself.” Species belonging to the same family or genus show higher similarity in all their characteristics between each other than to other less related species due to phylogenetic constraints (Raup and Gould 1974; Gould 2002). Therefore, species are more likely to be exploiting a similar resource base and acting as (from the ecosystem point of view) approximate functional equivalents of each other. This high initial similarity of competing interactors results in stiff competition and escalation that can either result in extinction or evolution of specialized morphologies due to so-called character displacement (Pfennig and Pfennig 2012). The described dynamics are not unlike those in artificial intelligence games, which self-master by playing against copies of themselves without any external supervision, as was implemented in the case of AlphaGo Zero, which achieved superhuman mastery of the ancient game of Go (Silver et al. 2017). Again, the greatest depth of coevolution and the greatest progress are expected in the largest geobiomes/Bretskyan units.

Integration by means of multiscale coevolution inside geobiomes is also an expected pattern for any set of taxa occupying

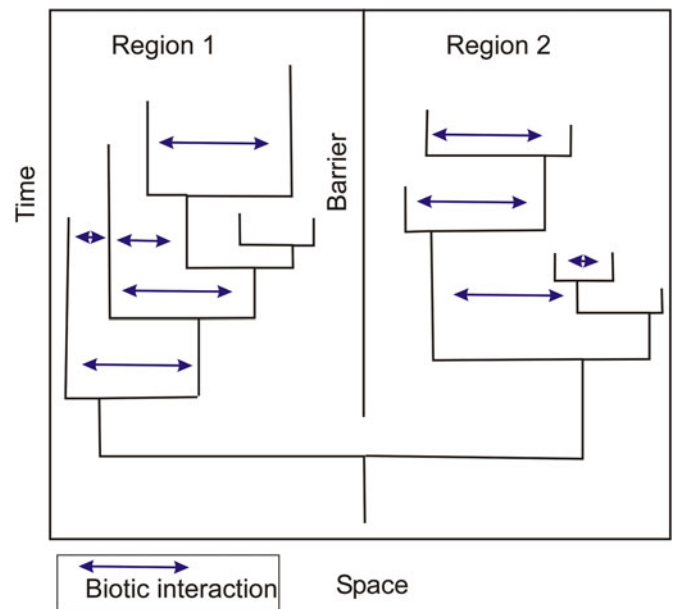


Figure 6. Clades separated for long periods of times will experience multiple rounds of competitive and other biotic interaction-mediated evolution inside the bioregions. This will increase the coadaptability of species in comparison to randomly drawn members of a clade from other regions.

the same bioregion (Fig. 7). Because selection and cross-optimization between different functional units should be more powerful in larger, longer-lasting, and more diverse bioregions, the geobiomes of these regions should be of higher resilience to external biotic and abiotic perturbations. Because it is expected that selection on ecosystems results in increased stability of ecosystems at all scales (Borrelli et al. 2015), we should expect a greater level of stability to perturbations to evolve in larger and longer-lasting Bretskyan units. The largest—the Gaian-level Bretskyan unit—is potentially eternal (up to the astrophysical limits); therefore, in the long run, it should achieve the maximal possible stability level. Empirical studies apparently confirm this pattern (Van Valen 1984; Foote 2000; Miller and Foote 2003; Markov 2009; Lieberman and Melott 2013).

Many aspects of evolution inside Bretskyan units can be conceptualized and understood using a generalization of fitness landscapes for geobiomes. In the case of geobiomes, instead of characters specific for Linnaean units such as organisms or species, we use characters that can describe geobiomes and holobionts in a meaningful way. These geobiome-scale phenotype variables can be, for example, average herbivore or average carnivore sizes in large vertebrate guilds (Fig. 8), variables describing ecological communities. These are essentially axes of ecospace (Novack-Gottshall 2016a,b) with quantitative gradations and fitness values assigned to them. The measurement of fitness in geobiomic fitness landscapes is a scaling concept, as are geobiomes themselves: different levels of inclusivity of traits are needed as we compare geobiomes of different scales. The many measurements of such combinations over long time periods should produce an estimate of geobiomic fitness landscape and reveal the directionality in evolution. A fine example of such an approach is the study that determined that Cenozoic North American mammals (or the mammalian component of the North American Cenozoic geobiome) have two body mass attractors (Alroy 1998a).

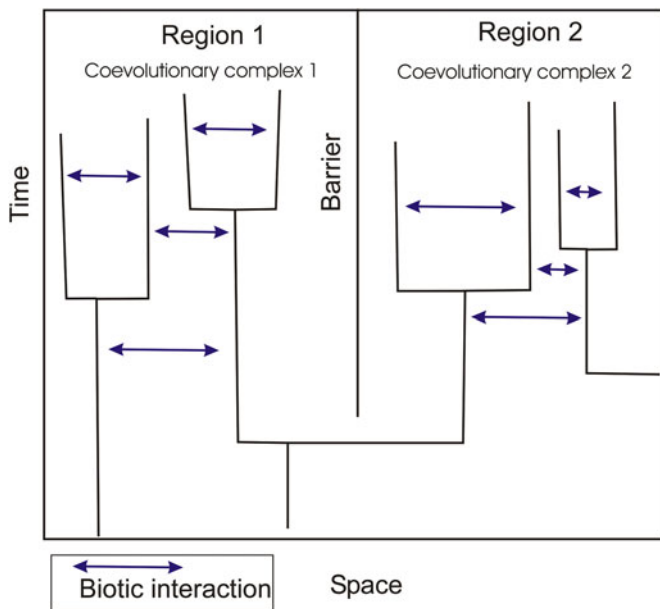


Figure 7. What is essentially the same process as in Fig. 6 works for mixtures of clades. Different regions separated from one another can receive invasions of different unrelated clades that will interact with the descendants of a given clade. This will create contingently different coevolutionary complexes (“splendid isolations” of George Gaylord Simpson’s “South Americas” [1983]). Here we have strong compartments that serve as robust individuating boundaries, not unlike reproductive isolation in the case of sexually reproducing species. Species evolution (selection and sorting) inside Bretskyan units should work analogous to natural selection inside species, but here we will have directional changes in the distribution of features of whole geobiomes—analogue to changes in average phenotypes of individual organisms inside their respective species, as happens at shorter time scales.

One of the major themes of evolution is the role of chance and contingency in the history of life (Gould 2001; Erwin 2016; Ramsey and Pence 2016). In his book *Wonderful Life*, Stephen Jay Gould argued that the extinction of body plans that were represented in the Cambrian by low numbers of species should have had a major consequence for all subsequent evolution, as it closed some major windows of evolutionary radiations and enabled some others represented by surviving phyla (Gould 1990). Whether or not the early extinctions in animal evolution had such a profound effect on macroevolution and ecology in the Phanerozoic, the temporal events arguably are of great importance in forming the composition and patterns of evolutionary dynamics (Jablonski 1986; Raup 1992, 1994; Brayard et al. 2009). The Bretskyan hierarchy worldview presents a generalization of evolutionary contingency in space–time.

Different states of a given biota can be separated by physical barriers of catastrophic conditions (mass extinctions events) in time, so too can parts of a biota be separated by physical barriers in space. The composition of clades before and after an extinction event can radically differ; also the composition of clades can differ in space. Depending on the composition of clades that are parts of geobiomes, any given geobiome could differ significantly in the shape of its fitness landscape, and therefore its vectors of evolutionary dynamics. For example, the fitness landscape of average masses of apex terrestrial vertebrate predators in the South American Miocene should have been very different from the fitness landscape of the North American geobiome. In the former case, South America was inhabited by members of four clades that filled that niche—metatherian sparassodont mammals,

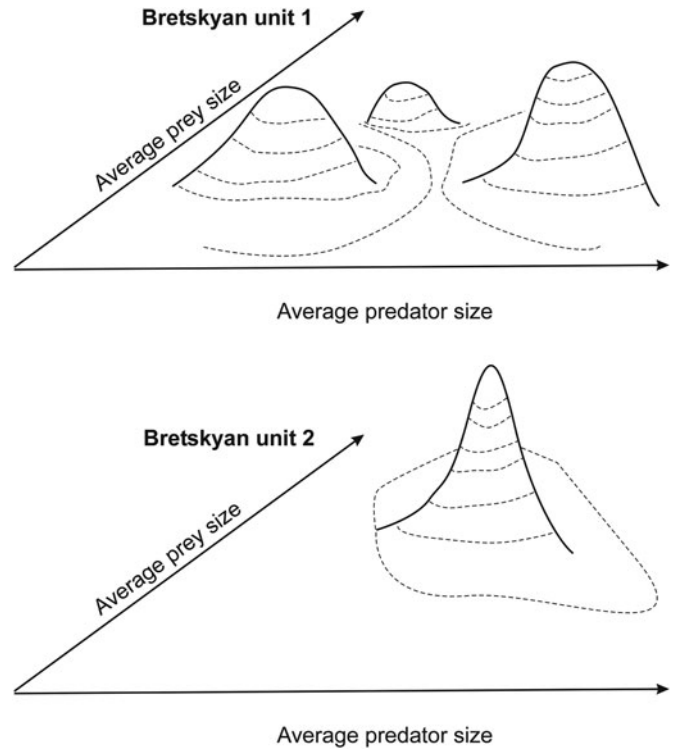


Figure 8. The concept of the fitness landscapes of large-scale Bretskyan units—geobiomes. In the case of grand spatial scales and grand geographic barriers that last tens to hundreds of millions of years, we are entering into the arena of grand evolutionary contingency. Sets of distinct taxa that populate bioregions after major extinction or origination events or as a result of prolonged isolation create very distinct geobiome-level fitness landscapes, attracting evolutionary change to highly distinct sets of parameter values. Shown here are two hypothetical examples: Bretskyan unit 1 could be imagined as representing the case of non-avian dinosaurs. Their anatomic characteristics, such as bone pneumaticity and egg laying, enabled an *r* strategy of population dynamics, which increases survivability of large animals in uncertain environments, so non-avian dinosaurs evolutionarily achieved much larger sizes than any terrestrial mammals (Sander and Clauss 2008; Sander et al. 2011; Botha et al. 2022). All these factors create boundary conditions for the emergence of radically different ecosystem fitness landscapes than in mammal-dominated ecosystems (represented by Bretskyan unit 2). Dinosaurs would evolve toward much larger predators and prey, and mammals would have optima at smaller body sizes. This difference in the real world happened in time and not in space, but this does not change the main conclusion. If non-avian dinosaurs, by any chance, had survived on some highly isolated continent, we currently would have had two very different geobiome fitness landscapes—one for mammals and the other for non-avian dinosaurs. The closest we currently have in the real world is the case of Australia vs. the rest of the inhabited continents. Here placental and marsupial mammals are highly distinct due to the presence of different developmental constraints (and their nature and importance for evolution can also change with time [Salazar-Ciudad et al. 2003])—marsupials probably will never develop truly marine species or flying or hoofed species, because their embryos need to have functional grabbing arms in order to get to the mother’s pouch (Sears 2004); moreover, the developmental constraints in marsupials have much wider effects (Fabre et al. 2021). The noted spatially contingent features constrain the ranges and directions of diversification inside the Bretskyan units and thus define their geobiome-level fitness landscapes.

terrestrial crocodiles, phorusrhacids or “terror birds,” and the giant snakes Madtsoiidae (Prevosti et al. 2013); while in the latter case, all top predators were placental mammals. Many other examples of the role of the space–time contingency in evolution could be given (Fig. 8).

The spatial structure of biodiversity implies the existence of scaling of contingency of evolution in space as well as in time as well as its limits. Endemicity and provincialism are always present, but at long time scales, species from different provinces

invade most environments suitable for their existence. Here tectonics and also climate fluctuations help the dispersal of taxa with different environmental tolerances and set limits on how different local and regional biotas can be and how long they can be effectively isolated (Spiridonov and Lovejoy 2022). The same kind of processes of merging of lower-level Bretskyan units after some time of isolation and forced individuality should be expected to proceed at all spatial and temporal scales—smaller spatial scales imply shorter time scales of merging and therefore shorter time scales of contingent evolution.

The last point of importance is evolutionary interaction and the question of mechanisms of selection of Bretskyan units. In the case of small-scale Bretskyan units (endosymbiotic cells, lichen, etc.), holobionts could be targets of Type II multilevel selection (MLS2; Damuth and Heisler 1988) when there are differences in reproductive capacities of holobionts themselves (“groups” produce more “groups”). In the case of large-scale Bretskyan units, which should have significant influence on the fitness of taxa residing and being part of their causal network, we should expect Type I multilevel selection (MLS1) when the differences in fitness reside in components of the groups (Damuth and Heisler 1988; Okasha 2006; Lean and Jones 2023). The special case here is the global holobiont-like unit Gaia (zu Castell et al. 2019), which is singular, the largest and indivisible in the long-term Bretskyan individual. The Gaian unit is modulating fitness of all lower-level units (Bourrat 2023) and also possesses its own fitness, defined here as resilience to its ultimate extinction—therefore it combines features of both Type I and Type II multilevel fitness. Contrary to popular conception and models that Gaia increases its chances of survival by means of regulation of environment (Lenton 1998; Arthur and Nicholson 2022), current evidence shows that such regulation is absent (Lovejoy 2015; Spiridonov and Lovejoy 2022), and life resists this unchecked change at the longest time scales (Spiridonov and Lovejoy 2022, 2023).

The effects of belonging to a given Bretskyan unit can be measured by differential survival or proliferation of taxa that originated in a geobiome. In this way, geobiomes do not produce more of the same geobiomes, as is the case for organism-level selection, but “successful” geobiomes make future geobiomes resemble them compositionally (Fig. 9). The merging of Bretskyan units during collision results in multiple invasions (Stigall 2019) that are natural experiments that can be used in testing of hierarchical scaling laws of spatiotemporal evolution of geobiomes at large scales. One of the finest and best-researched examples of such mergers of large Bretskyan units is GABI, which happened in the late Cenozoic between North America and South America (Marshall et al. 1982). Apparently South American mammalian faunas experienced higher extinction rates in comparison to North American mammalian faunas (Carrillo et al. 2020), which is in line with expectations of larger and more environmentally diverse geobiomes having higher competitiveness.

Apparently, as was shown by the case studies of modern South and North American freshwater fishes, the diversity history and the distribution of species richness is significantly affected by dynamics of sub-continental structures, even at scales of millions to tens of millions of years, thus showing the great influence of Bretskyan units in molding some of the most recent evolutionary radiations (Cassemiro et al. 2023; Stokes et al. 2023). Therefore, we can see that fragmentation and dynamics of landscapes at multiple spatiotemporal scales are crucial in modulating small-scale

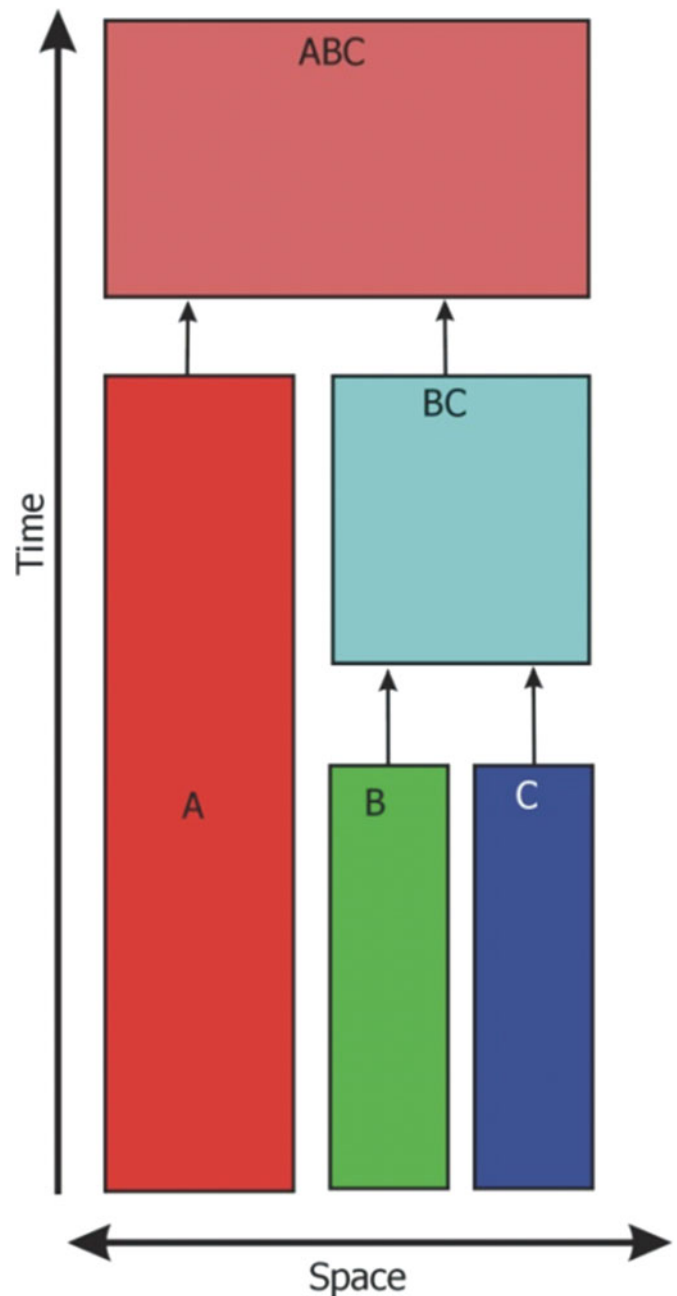


Figure 9. Interactions between higher-level geobiomes, here representing hypothetical bioprovinces experiencing sequential fusion events; these could be large islands or terrains isolated by a sea that merge sequentially during eustatic regression. Compositions of bioprovinces are represented by colors. Type I multilevel selection (MLS1) Bretskyan fitness of provinces B and C is equal (competitive ability of component taxa is the same); therefore, the newly merged unit BC has exactly intermediate composition. Bretskyan unit A has much higher fitness than unit BC; therefore its taxa dominate unit ABC, which is formed by the final merger.

taxonomic changes, as well as changes in whole faunas—the mosaic of evolution and its coordination is sustained and reshaped by branching (multiscale allopatry) and merging (or the Geo-Red Queen [Spiridonov and Lovejoy 2022]) of landscapes by means of tectonic geodynamics and climate change.

Many more such studies across many clades, areas, times, and time scales (Patzkowsky 2017; Stigall et al. 2017) are needed, including cases of geographic differences in recoveries after

mass extinctions and other significant events (Jablonski 2005), in order to generalize the patterns of evolution and to derive scaling laws applicable to different levels of the Bretskyan hierarchy.

The major purpose of this paper is the explication of the basic biological ontology across all scales. Nonetheless, the described properties of the Bretskyan units and the processes that determine and form the Bretskyan hierarchy at large scales of geobiomes present a range of empirical predictions that, as in the case of the “first law of biology” (McShea and Brandon 2010), should be understood as idealized patterns, which can be best detected at *ceteris paribus* conditions. Predictions listed here are related to the greater coevolutionary depth of taxa and greater match to a wider range of environments with which taxa interacted in space and time while being part of larger, older, and more structured geobiomes (by possessing more of the Fisherian information and consequently being more “learned” and more integrated with each other) than in smaller, younger, and less complex geobiomes. These are, upon fusion of geobiomes: (1) taxa from larger/older geobiomes will on average occupy a wider range of environments; (2) taxa from larger/older geobiomes will have higher chances of invasion and establishment; (3) taxa from larger/older geobiomes will be found in ecological associations more frequently and for longer geological time; (4) taxa from geodynamically more active/complex regions (more spatiotemporally structured geobiomes) should exhibit higher fitness given the same area, climate, and the age of a geobiome; (5) taxa from larger/older geobiomes should have longer survivorship half-lives; and (6) average duration of a taxon should increase as time passes in a given geobiome, consequently if sampled at arbitrary time (e.g., recent), the average taxon ages should be longer in an older/larger geobiome (e.g., marine vs. terrestrial geobiomes).

Regarding prediction 2: The modern ecosystems that are highly influenced by anthropogenic factors are affected by massive influx of invasive species (Stigall 2019), the most disruptive of which is arguably humans. The Bretskyan hierarchy approach gives a predictive framework on how this increased dispersal (or fusion of multiscale geobiomes) event can proceed. Predictions span the whole range of time scales, from immediate establishment, to the environmental breadth of dispersal, to ultimately the differential evolutionary success of the invaders. The same principles could be cross-tested in deep-time settings, thus providing deeper insights into strength of geobiomic factors in ecology and evolution.

Conclusions

Conceptual analysis of the Bretskyan hierarchy reveals a comprehensive framework for understanding and describing ecogenealogical units. In contrast, the purely economic hierarchy lacks perspective on the common evolutionary fates of constituent ecological interactors. Likewise, the Linnaean hierarchy also shows significant limitations to comprehensive understanding of the ontologies of the biological world (Van Valen 1978, 1984). The Linnaean hierarchy is completely divorced from space and only implicitly tied to time. It is, rather, simply a scorecard of relative success of genotypes, phenotypes, and thereby monophyletic taxa of all ranks. The Bretskyan hierarchy represents a fusion and fission hierarchy of spatially and temporally compartmentalized communities that share common histories of causal interactions, resulting in coevolution, and their integration inside lineage-like Bretskyan units that are ontological individuals with spatial ranges and time spans. Also the Bretskyan hierarchy, together with the Linnaean

hierarchy, absorbs the theme of the major transitions in evolution under a single hierarchical theoretical framework in which egalitarian transitions represent processes of the emergence of evolutionary individuality in the former hierarchy and fraternal transitions represent similar processes in the lower tiers of the latter.

The Bretskyan hierarchy is formed at all time and space scales by the hierarchy of isolating factors that are fundamentally related to the structuring of the environment. Multiscale allopatry by geological barriers at shorter time scales encompasses a subset of species-level allopatry, but the same principle of geodynamic isolation applies for whole geobiomes. Spatial isolation compartmentalizes biotas at all levels and controls the tempos and scales of coevolution inside isolated Bretskyan units, while also determining the tempos of their coordination ensured by gene flow and geodispersal more generally (Lieberman and Eldredge 1996). These facts imply that biology in its essence, including modes of origin and evolution, is deeply geological and geophysical.

The Bretskyan hierarchy is the missing link between functional and genealogical hierarchies and combines the features of both—(1) ecological causality, which is the driver of evolutionary change, is acknowledged to happen in co-occupied space and time; while (2) the temporal continuity of compartments of Bretskyan units implies phylogeny-like patterns for communities of interactors (for which taxonomic rank could differ depending on the scale of the geobiome). The Bretskyan hierarchy perspective allows explicit spatiotemporal understanding of contingency in evolution by acknowledging the importance of spatial and temporal compartmentalization of parts of biotas. This enables a hierarchy of parallel natural experiments at multiple times and time scales. The realization that the Bretskyan hierarchy in time represents an anastomosing multiscale network-like structure also explicitly sets limits to the time and space scales of contingency in evolution inside the biota.

The Bretskyan hierarchy paradigm of biotic evolution also sets a range of predictions on the scaling of the progress and competitiveness of component taxa and relates the issue of progress to geodynamics. The spatial structures and time scales and the processes spanning them are intrinsically related by scaling laws, which also transcend biology and originate in geology. The Bretskyan hierarchy of holobionts and geobiomes explicitly acknowledges this reality and suggests explanations for a range of known patterns and also suggests a range of conjectures to test with empirical data. It suggests a unified and multifaceted framework for understanding the rates and the character of evolutionary change on all scales throughout the duration of an entire planet.

In sum, the Bretskyan hierarchy is based on the existence of real-world, real-time entities that are fusions of the simultaneous, yet separable, twin processes of life: economic (energy–matter transfer) processes and genealogical (production of more entities of like kind) patterns. In short, the Bretskyan hierarchy is a real-world, empirical ontology of living systems of all scales, and their relation to the abiotic realm.

Acknowledgments. We would like to thank R. Stankevič and S. Newman for discussion on earlier versions of this paper, and we thank editor J. Crampton, and also C. Simpson and an anonymous reviewer for comments that significantly improved the content and the clarity of this paper. A.S. would like to thank his daughter E. S. Spiridonova for accompanying him on long walks around Vilnius that deeply stimulated thinking about the space, scales, and evolution. This research was supported by the project S-MIP-21-9 “The Role of Spatial Structuring in Major Transitions in Macroevolution.”

Competing Interests. The authors declare no competing interests.

Literature Cited

- Aarssen, L. W., and R. Turkington. 1983. What is community evolution? *Evolutionary Theory* 6:211–217.
- Aberhan, M., and W. Kiessling. 2015. Persistent ecological shifts in marine molluscan assemblages across the end-Cretaceous mass extinction. *Proceedings of the National Academy of Sciences USA* 112:7207–7212.
- Allen, T. F. H., and T. B. Starr. 1982. *Hierarchy: perspectives for ecological complexity*. University of Chicago Press Chicago, Chicago.
- Allmon, W. D., and S. D. Sampson. 2016. The stages of speciation: a stepwise framework for analysis of speciation in the fossil record. Pp. 121–167 in W. D. Allmon and M. M. Yacobucci, eds. *Species and speciation in the fossil record*. University of Chicago Press, Chicago.
- Allmon, W., P. J. Morris, and M. L. McKinney. 1998. An intermediate disturbance hypothesis of maximal speciation. Pp. 349–376 in M. L. McKinney and J. A. Drake, eds. *Biodiversity dynamics: turnover of populations, taxa and communities*. Columbia University Press, New York.
- Alroy, J. 1998a. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science* 280:731–734.
- Alroy, J. 1998b. Diachrony of mammalian appearance events: implications for biochronology. *Geology* 26:23–26.
- Alroy, J. 2010. The shifting balance of diversity among major marine animal groups. *Science* 329:1191–1194.
- Alvarez, L. W., W. Alvarez, F. Asaro, and H. V. Michel. 1980. Extraterrestrial cause for the Cretaceous–Tertiary extinction. *Science* 208:1095–1108.
- Anderson, T. H. 2022. Plate convergence, consumption, collision, coupling, capture, and formation of mantle waves—linkages to global orogenesis and epeirogeny. In G. R. Foulger, L. C. Hamilton, D. M. Jurdy, C. A. Stein, K. A. Howard, and S. Stein, eds. *In the footsteps of Warren B. Hamilton: new ideas in Earth science*. Geological Society of America Special Paper 553:137–158.
- Anderson, S. A. S., and J. T. Weir. 2022. The role of divergent ecological adaptation during allopatric speciation in vertebrates. *Science* 378:1214–1218.
- Archibald, S. B., W. H. Bossert, D. R. Greenwood, and B. D. Farrell. 2010. Seasonality, the latitudinal gradient of diversity, and Eocene insects. *Paleobiology* 36:374–398.
- Arnold, M. L. 2006. *Evolution through genetic exchange*. Oxford University Press, Oxford.
- Arthur, R., and A. Nicholson. 2022. Selection principles for Gaia. *Journal of Theoretical Biology* 533:110940.
- Bambach, R. K. 2006. Phanerozoic biodiversity mass extinctions. *Annual Reviews of Earth and Planetary Sciences* 34:127–155.
- Bambach, R. K., and J. B. Bennington. 1996. Do communities evolve? A major question in evolutionary paleoecology. Pp. 123–160 in D. Jablonski, D. H. Erwin, and J. H. Lipps, eds. *Evolutionary paleobiology*. University of Chicago Press, Chicago.
- Bapteste, E., P. Lopez, F. Bouchard, F. Baquero, J. O. McInerney, and R. M. Burian. 2012. Evolutionary analyses of non-genealogical bonds produced by introgressive descent. *Proceedings of the National Academy of Sciences USA* 109:18266–18272.
- Bennington, J. B., W. A. Dimichele, C. Badgley, R. K. Bambach, P. M. Barrett, A. K. Behrensmeyer, R. Bobe, et al. 2009. Critical issues of scale in paleoecology. *Palaïos* 24:1–4.
- Bickerton, D. 2009. *Adam's tongue: how humans made language, how language made humans*. Hill and Wang, New York.
- Björck, S. 1995. A review of the history of the Baltic Sea, 13.0–8.0 ka BP. *Quaternary International* 27:19–40.
- Borrelli, J. J., S. Allesina, P. Amarasekare, R. Arditi, I. Chase, J. Damuth, R. D. Holt, et al. 2015. Selection on stability across ecological scales. *Trends in Ecology and Evolution* 30:417–425.
- Botha, J., J. N. Choiniere, and R. B. Benson. 2022. Rapid growth preceded gigantism in sauropodomorph evolution. *Current Biology* 32:4501–4507.e2.
- Bouchard, F. 2014. Ecosystem evolution is about variation and persistence, not populations and reproduction. *Biological Theory* 9:382–391.
- Bourke, A. F. G. 2011. *Principles of social evolution*. Oxford University Press, Oxford.
- Bourrat, P. 2023. A Pricean formalization of Gaia. *Philosophy of Science* 90:704–720.
- Brandon, R. N., and D. W. McShea. 2020. *The missing two-thirds of evolutionary theory*. Cambridge University Press, Cambridge.
- Brayard, A., G. Escarguel, H. Bucher, C. Monnet, T. Brühwiler, N. Goudemand, T. Galfetti, and J. Guex. 2009. Good genes and good luck: ammonoid diversity and the end-Permian mass extinction. *Science* 325:1118–1121.
- Bretsky, P. W. 1968. Evolution of Paleozoic marine invertebrate communities. *Science* 159:1231–1233.
- Brett, C. E., and G. C. Baird. 1995. Coordinated stasis and evolutionary ecology of Silurian to Middle Devonian faunas in the Appalachian Basin. Pp. 285–315 in D. H. Erwin, and R. L. Anstey, eds. *New approaches to speciation in the fossil record*. Columbia University Press, New York.
- Brett, C. E., L. C. Ivany, and K. M. Schopf. 1996. Coordinated stasis: an overview. *Palaeogeography, Palaeoclimatology, Palaeoecology* 127(1–4):1–20.
- Brombacher, A., P. A. Wilson, I. Bailey, and T. Ezard. 2023. Morphological variation across space does not predict phenotypic change through time in two Neogene planktonic foraminifera species. *Frontiers in Ecology and Evolution* 11. <https://doi.org/10.3389/fevo.2023.1165174>.
- Brown, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago.
- Buss, L. W. 1987. *Evolution of individuality*. Princeton University Press, Princeton, N.J.
- Calcott, B., and K. E. Sterelny. 2011. *The major transitions in evolution revisited*. MIT Press, Cambridge, Mass.
- Carrillo, J. D., S. Faurby, D. Silvestro, A. Zizka, C. Jaramillo, C. D. Bacon, and A. Antonelli. 2020. Disproportionate extinction of South American mammals drove the asymmetry of the Great American Biotic Interchange. *Proceedings of the National Academy of Sciences USA* 117:26281–26287.
- Casemiro, F. A., J. S. Albert, A. Antonelli, A. Menegotto, R. O. Wüest, F. Cerezer, M. T. P. Coelho, R. E. Reis, M. Tan, and V. Tagliacollo. 2023. Landscape dynamics and diversification of the megadiverse South American freshwater fish fauna. *Proceedings of the National Academy of Sciences USA* 120:e2211974120.
- Catuneanu, O. 2006. *Principles of sequence stratigraphy*. Elsevier, Amsterdam.
- Clague, D. A., and G. B. Dalrymple. 1987. The Hawaiian–Emperor volcanic chain, Part I. *U.S. Geological Survey Professional Paper* 1350:5–54.
- Cooper, R. A., and P. M. Sadler. 2010. Facies preference predicts extinction risk in Ordovician graptolites. *Paleobiology* 36:167–187.
- Cracraft, J. 1982. A nonequilibrium theory for the rate-control of speciation and extinction and the origin of macroevolutionary patterns. *Systematic Zoology* 31:348–365.
- Crampton, J. S., S. R. Meyers, R. A. Cooper, P. M. Sadler, M. Foote, and D. Harte. 2018. Pacing of Paleozoic macroevolutionary rates by Milankovitch grand cycles. *Proceedings of the National Academy of Sciences USA* 115:5686–5691.
- Crampton, J. S., R. A. Cooper, M. Foote, and P. M. Sadler. 2020. Ephemeral species in the fossil record? Synchronous coupling of macroevolutionary dynamics in mid-Paleozoic zooplankton. *Paleobiology* 46:123–135.
- Currie, A. 2019. Mass extinctions as major transitions. *Biology and Philosophy* 34:29.
- Cuthill, J. F. H., N. Guttenberg, and G. E. Budd. 2020. Impacts of speciation and extinction measured by an evolutionary decay clock. *Nature* 588:636–641.
- Czárán, T., and E. Szathmáry. 2000. Coexistence of replicators in prebiotic evolution. Pp. 116–134 in U. Dieckmann, R. Law, and J. A. J. Metz, eds. *The geometry of ecological interactions: simplifying spatial complexity* (Cambridge Studies in Adaptive Dynamics). Cambridge University Press, Cambridge.
- Damuth, J., and I. L. Heisler. 1988. Alternative formulations of multilevel selection. *Biology and Philosophy* 3:407–430.
- Darwin, C. 1839. *Journal of Researches into the Geology and Natural History of the various countries visited by H.M.S. Beagle* by Charles Darwin (1839). Hefner Publishing, New York/London, repr. 1952.

- de Castro, C., and D. W. McShea. 2022. Applying the Prigogine view of dissipative systems to the major transitions in evolution. *Paleobiology* 48:711–728.
- DeGregori, J., and N. Eldredge. 2020. Parallel causation in oncogenic and anthropogenic degradation and extinction. *Biological Theory* 15:12–24.
- Descamps-Julien, B., and A. Gonzalez. 2005. Stable coexistence in a fluctuating environment: an experimental demonstration. *Ecology* 86:2815–2824.
- Dieckmann, U., R. Law, J. A. J. Metz, eds. 2000. *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge University Press, New York.
- Dobzhansky, T. 1937. Genetic nature of species differences. *American Naturalist* 71:404–420.
- Dobzhansky, T. 1940. Speciation as a stage in evolutionary divergence. *American Naturalist* 74:312–321.
- Edelstein-Keshet, L. 2005. *Mathematical models in biology*. SIAM, Philadelphia.
- Eichenseer, K., U. Balthasar, C. W. Smart, J. Stander, K. A. Haaga, and W. Kiessling. 2019. Jurassic shift from abiotic to biotic control on marine ecological success. *Nature Geoscience* 12:638–642.
- Eldredge, N. 1971. The allopatric model and phylogeny in Paleozoic invertebrates. *Evolution* 25:156–167.
- Eldredge, N. 1985. *Unfinished synthesis: biological hierarchies and modern evolutionary thought*. Oxford University Press, New York.
- Eldredge, N. 1986. Information, economics, and evolution. *Annual Review of Ecology and Systematics* 17:351–369.
- Eldredge, N. 1989. *Macroevolutionary dynamics: species, niches & adaptive peaks*. McGraw-Hill, New York.
- Eldredge, N. 1995. *Reinventing Darwin: the great evolutionary debate*. Weidenfeld and Nicolson, London.
- Eldredge, N. 1996. Hierarchies in macroevolution. Pp. 42–61 in D. Jablonski, D. H. Erwin, and J. H. Lipps, eds. *Evolutionary paleobiology*. University of Chicago Press, Chicago.
- Eldredge, N. 1999. *The pattern of evolution*. Freeman, New York.
- Eldredge, N. 2003. The sloshing bucket: how the physical realm controls evolution. Pp. 3–32 in J. P. Crutchfield and P. Schuster, eds. *Evolutionary dynamics: exploring the interplay of selection, accident, neutrality, and function* (SFI Studies in the Sciences of Complexity Series). Oxford University Press, New York.
- Eldredge, N. 2008. Hierarchies and the sloshing bucket: toward the unification of evolutionary biology. *Evolution: Education and Outreach* 1:10–15.
- Eldredge, N. 2009. Material cultural macroevolution. Pp. 297–316 in A. Prentiss, I. Kuijt, and J. Chatters, eds. *Macroevolution in human prehistory*. Springer, New York.
- Eldredge, N., and S. J. Gould. 1972. Punctuated equilibria: an alternative to phyletic gradualism. Pp. 82–115 in T. Schopf, ed. *Models in paleobiology*. Freeman and Company, San Francisco.
- Eldredge, N., and S. N. Salthé. 1984. Hierarchy and evolution. Pp. 184–208 in R. Dawkins and M. Ridley, eds. *Oxford surveys in evolutionary biology*. Oxford University Press, Oxford.
- Eldredge, N., J. N. Thompson, P. M. Brakefield, S. Gavrillets, D. Jablonski, J. B. C. Jackson, R. E. Lenski, B. S. Lieberman, M. A. McPeck, and W. Miller. 2005. The dynamics of evolutionary stasis. *Paleobiology* 31 (S2):133–145.
- Erwin, D. H. 2016. *Wonderful Life* revisited: chance and contingency in the Ediacaran-Cambrian radiation. Pp. 279–298 in G. Ramsey and C. H. E. Pence, eds. *Chance in evolution*. University of Chicago Press, Chicago.
- Fabre, A.-C., C. Dowling, R. Portela Miguez, V. Fernandez, E. Noirault, and A. Goswami. 2021. Functional constraints during development limit jaw shape evolution in marsupials. *Proceedings of the Royal Society of London B* 288:20210319.
- Finnegan, S., N. A. Heim, S. E. Peters, and W. W. Fischer. 2012. Climate change and the selective signature of the Late Ordovician mass extinction. *Proceedings of the National Academy of Sciences USA* 109:6829–6834.
- Flynn, J. J., B. J. MacFadden, and M. C. McKenna. 1984. Land-mammal ages, faunal heterochrony, and temporal resolution in Cenozoic terrestrial sequences. *Journal of Geology* 92:687–705.
- Foote, M. 2000. Origination and extinction components of taxonomic diversity: general problems. *Paleobiology* 26(S4):74–102.
- Foote, M. 2005. Pulsed origination and extinction in the marine realm. *Paleobiology* 40:6–20.
- Frank, S. A. 2009. Natural selection maximizes Fisher information. *Journal of Evolutionary Biology* 22:231–244.
- Futuyma, D. J. 1987. On the role of species in anagenesis. *American Naturalist* 130:465–473.
- Gagnon, J.-S., S. Lovejoy, and D. Schertzer. 2006. Multifractal earth topography. *Nonlinear Processes in Geophysics* 13:541–570.
- Gavrilets, S. 2004. *Fitness landscapes and the origin of species* (Monographs in Population Biology 41). Princeton University Press, Princeton, N.J.
- Gilbert, S. F., and A. I. Tauber. 2016. Rethinking individuality: the dialectics of the holobiont. *Biology and Philosophy* 31:839–853.
- Godfrey-Smith, P. 2009. *Darwinian populations and natural selection*. Oxford University Press, Oxford.
- Gould, S. J. 1980. Is a new and general theory of evolution emerging? *Paleobiology* 6:119–130.
- Gould, S. J. 1985. The paradox of the first tier: an agenda for paleobiology. *Paleobiology* 11:2–12.
- Gould, S. J. 1990. *Wonderful life: the Burgess Shale and the nature of history*. Norton, New York.
- Gould, S. J. 2001. Contingency. Pp. 195–198 in D. E. G. Briggs and P. R. Crowther, eds. *Palaeobiology II*. Blackwell Science, Malden, Mass.
- Gould, S. J. 2002. *The structure of evolutionary theory*. Harvard University Press, Cambridge, Mass.
- Gould, S. J., and R. F. Johnston. 1972. Geographic variation. *Annual Review of Ecology and Systematics* 3:457–498.
- Gould, S. J., and E. A. Lloyd. 1999. Individuality and adaptation across levels of selection: How shall we name and generalize the unit of Darwinism? *Proceedings of the National Academy of Sciences USA* 96:11904–11909.
- Hernández-Hernández, T., E. C. Miller, C. Román-Palacios, and J. J. Wiens. 2021. Speciation across the tree of life. *Biological Reviews* 96:1205–1242.
- Hoffman, A. 1979. Community paleoecology as an epiphenomenal science. *Paleobiology* 5:357–379.
- Holyoak, M., M. A. Leibold, N. Mouquet, R. D. Holt, and M. Hoopes. 2005. A framework for large scale community ecology. Pp. 1–31 in M. Holyoak, M. A. Leibold, and R. D. Holt, eds. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago.
- Hunt, G. 2007. The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. *Proceedings of the National Academy of Sciences USA* 104:18404–18408.
- Hutchinson, G. E. 1961. The paradox of the plankton. *American Naturalist* 95:137–145.
- Ivany, L. C., C. E. Brett, H. L. B. Wall, P. D. Wall, and J. C. Handley. 2009. Relative taxonomic and ecologic stability in Devonian marine faunas of New York State: a test of coordinated stasis. *Paleobiology* 35:499–524.
- Jablonski, D. 1986. Background and mass extinctions: the alternation of macroevolutionary regimes. *Science* 231:129–133.
- Jablonski, D. 2005. Mass extinctions and macroevolution. *Paleobiology* 31 (S5):192–210.
- Jablonski, D. 2007. Scale and hierarchy in macroevolution. *Palaeontology* 50:87–109.
- Jablonski, D. 2008a. Extinction and the spatial dynamics of biodiversity. *Proceedings of the National Academy of Sciences USA* 105(Suppl 1):11528–11535.
- Jablonski, D. 2008b. Species selection: theory and data. *Annual Review of Ecology, Evolution, and Systematics* 39:501–524.
- Jablonski, D. 2017. Approaches to macroevolution. 2. Sorting of variation, some overarching issues, and general conclusions. *Evolutionary Biology* 44:451–475.
- Kay, M., and N. Eldredge. 1968. Cambrian trilobites in central Newfoundland volcanic belt. *Geological Magazine* 105:372–377.
- Kazlauskas, D., A. Varsani, E. V. Koonin, and M. Krupovic. 2019. Multiple origins of prokaryotic and eukaryotic single-stranded DNA viruses from bacterial and archaeal plasmids. *Nature Communications* 10:3425.
- Kenrick, P., C. H. Wellman, H. Schneider, and G. D. Edgecombe. 2012. A timeline for terrestrialization: consequences for the carbon cycle in the Palaeozoic. *Philosophical Transactions of the Royal Society of London B* 367:519–536.

- Kiessling, W. 2009. Geologic and biologic controls on the evolution of reefs. *Annual Review of Ecology, Evolution, and Systematics* 40:173–192.
- Knoll, A. H., and R. K. Bambach. 2000. Directionality in the history of life: diffusion from the left wall or repeated scaling of the right? *Paleobiology* 26(S4):1–14.
- Knoll, A. H., and M. A. Nowak. 2017. The timetable of evolution. *Science Advances* 3:e1603076.
- Koonin, E. V., and K. S. Makarova. 2019. Origins and evolution of CRISPR-Cas systems. *Philosophical Transactions of the Royal Society of London B* 374:20180087.
- Krug, A. Z., D. Jablonski, and J. W. Valentine. 2009. Signature of the end-Cretaceous mass extinction in the modern biota. *Science* 323:767–771.
- Lakovic, M., and M. C. Rillig. 2022. A nuclei-based conceptual model of (eco) evolutionary dynamics in fungal heterokaryons. *Frontiers in Microbiology* 13. <https://doi.org/10.3389/fmicb.2022.914040>.
- Landais, F., F. Schmidt, and S. Lovejoy. 2019. Multifractal topography of several planetary bodies in the solar system. *Icarus* 319:14–20.
- Lean, C. H., and C. J. Jones. 2023. The evolution of multispecies populations: a multilevel selection perspective. *Biology and Philosophy* 38. <https://doi.org/10.1007/s10539-023-09929-7>.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- Lekevičius, E. 2006. The Russian paradigm in ecology and evolutionary biology: pro et contra. *Acta Zoologica Lituanica* 16(1):3–19.
- Lenton, T. M. 1998. Gaia and natural selection. *Nature* 394:439–447.
- Lenton, T. M., T. W. Dahl, S. J. Daines, B. J. W. Mills, K. Ozaki, M. R. Saltzman, and P. Porada. 2016. Earliest land plants created modern levels of atmospheric oxygen. *Proceedings of the National Academy of Sciences USA* 113:9704–9709.
- Levins, R., and R. C. Lewontin. 1987. *The dialectical biologist*. Harvard University Press, Cambridge, Mass.
- Lewontin, R. C. 1970. The units of selection. *Annual Review of Ecology and Systematics* 1:1–18.
- Lieberman, B. S. 2003. Paleobiogeography: the relevance of fossils to biogeography. *Annual Review of Ecology, Evolution, and Systematics* 34:51–69.
- Lieberman, B. S., and N. Eldredge. 1996. Trilobite biogeography in the Middle Devonian: geological processes and analytical methods. *Paleobiology* 22:66–79.
- Lieberman, B. S., and A. L. Melott. 2007. Considering the case for biodiversity cycles: re-examining the evidence for periodicity in the fossil record. *PLoS ONE* 2:e759.
- Lieberman, B. S., and A. L. Melott. 2013. Declining volatility, a general property of disparate systems: from fossils, to stocks, to the stars. *Palaeontology* 56:1297–1304.
- Lieberman, B. S., and E. S. Vrba. 2005. Stephen Jay Gould on species selection: 30 years of insight. *Paleobiology* 31(S2):113–121.
- Lieberman, B. S., C. E. Brett, and N. Eldredge. 1995. A study of stasis and change in two species lineages from the Middle Devonian of New York State. *Paleobiology* 21:15–27.
- Lieberman, B. S., W. Miller III, and N. Eldredge. 2007. Paleontological patterns, macroecological dynamics and the evolutionary process. *Evolutionary Biology* 34:28–48.
- Lloyd, E. A. 1994. *The structure and confirmation of evolutionary theory*. Princeton University Press, Princeton, N.J.
- Lloyd, E. A., and S. J. Gould. 1993. Species selection on variability. *Proceedings of the National Academy of Sciences USA* 90:595–599.
- Lovejoy, S. 2015. A voyage through scales, a missing quadrillion and why the climate is not what you expect. *Climate Dynamics* 44:3187–3210.
- Lovejoy, S. 2018. Spectra, intermittency, and extremes of weather, macro-weather and climate. *Scientific Reports* 8:1–13.
- Lovejoy, S., and D. Schertzer. 2013. *The weather and climate: emergent laws and multifractal cascades*. Cambridge University Press, New York.
- Margulis, L., and D. Bermudes. 1985. Symbiosis as a mechanism of evolution: status of cell symbiosis theory. *Symbiosis* 1:101–124.
- Margulis, L., M. F. Dolan, and J. H. Whiteside. 2005. “Imperfections and oddities” in the origin of the nucleus. *Paleobiology* 31(S2):175–191.
- Markov, A. V. 2009. Alpha diversity of Phanerozoic marine communities positively correlates with longevity of genera. *Paleobiology* 35:231–250.
- Marshall, C. R. 2006. Explaining the Cambrian “explosion” of animals. *Annual Review of Earth and Planetary Sciences* 34:355–384.
- Marshall, C. R. 2023. Forty years later: The status of the “Big Five” mass extinctions. *Cambridge Prisms: Extinction* 1:e5.
- Marshall, L. G., S. D. Webb, J. J. Sepkoski, and D. M. Raup. 1982. Mammalian evolution and the great American interchange. *Science* 215:1351–1357.
- Mathes, G. H., J. van Dijk, W. Kiessling, and M. J. Steinbauer. 2021. Extinction risk controlled by interaction of long-term and short-term climate change. *Nature Ecology and Evolution* 5:304–310.
- Maynard Smith, J., and E. Szathmáry. 1998. *The major transitions in evolution*. Oxford University Press, Oxford.
- Mayr, E. 1940. Speciation phenomena in birds. *American Naturalist* 74:249–278.
- McGhee, G. R. 2006. *The geometry of evolution: adaptive landscapes and theoretical morphospaces*. Cambridge University Press, Cambridge.
- McGill, B. J., J. M. Chase, J. Hortal, I. Overcast, A. J. Rominger, J. Rosindell, P. A. Borges, B. C. Emerson, R. Etienne, and M. J. Hickerson. 2019. Unifying macroecology and macroevolution to answer fundamental questions about biodiversity. *Global Ecology and Biogeography* 28:1925–1936.
- McKenna, M. C. 1972. Possible biological consequences of plate tectonics. *BioScience* 22:519–525.
- McShea, D. W., and R. N. Brandon. 2010. *Biology’s first law: the tendency for diversity and complexity to increase in evolutionary systems*. University of Chicago Press, Chicago.
- Meyers, S. R., and S. E. Peters. 2011. A 56 million year rhythm in North American sedimentation during the Phanerozoic. *Earth and Planetary Science Letters* 303:174–180.
- Miall, A. D. 2010. *The geology of stratigraphic sequences*, 2nd ed. Springer, Berlin.
- Miller, A. I., and M. Foote. 2003. Increased longevity of post-Paleozoic marine genera after mass extinctions. *Science* 302:1030–1032.
- Murchison, E. P., C. Tovar, A. Hsu, H. S. Bender, P. Kheradpour, C. A. Rebbeck, D. Obendorf, C. Conlan, M. Bahlo, and C. A. Blizzard. 2010. The Tasmanian devil transcriptome reveals Schwann cell origins of a clonally transmissible cancer. *Science* 327:84–87.
- Murphy, M. A., and A. Salvador. 1999. International stratigraphic guide—an abridged version. *Episodes: Journal of International Geoscience* 22:255–271.
- Nance, R. D. 2022. The supercontinent cycle and Earth’s long-term climate. *Annals of the New York Academy of Sciences* 1515:33–49.
- Niklas, K. J. 2004. Computer models of early land plant evolution. *Annual Review of Earth and Planetary Sciences* 32:47–66.
- Novack-Gottshall, P. M. 2016a. General models of ecological diversification. I. Conceptual synthesis. *Paleobiology* 42:185–208.
- Novack-Gottshall, P. M. 2016b. General models of ecological diversification. II. Simulations and empirical applications. *Paleobiology* 42:209–239.
- Nowak, M. A., and H. Ohtsuki. 2008. Prevolutionary dynamics and the origin of evolution. *Proceedings of the National Academy of Sciences USA* 105:14924–14927.
- Nowak, M. A., C. E. Tarnita, and E. O. Wilson. 2010. The evolution of eusociality. *Nature* 466:1057–1062.
- Ogg, J. G., G. Ogg, and F. M. Gradstein. 2008. *The concise geologic time scale*. Cambridge University Press, Cambridge.
- Okasha, S. 2006. *Evolution and the levels of selection*. Clarendon Press, Oxford.
- Okasha, S. 2012. Emergence, hierarchy and top-down causation in evolutionary biology. *Interface Focus* 2:49–54.
- O’Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. *A hierarchical concept of ecosystems*. Princeton University Press, Princeton.
- Palamara, G. M., A. Rozenfeld, C. N. de Santana, J. Klecka, R. Riera, V. M. Eguíluz, and C. J. Melián. 2023. Biodiversity dynamics in landscapes with fluctuating connectivity. *Ecography* 2023:e06385.
- Paterson, H. E. H. 1985. The recognition concept of species. Pp. 21–29 in E. S. Vrba, ed. *Species and speciation* (Transvaal Museum Monograph). Transvaal Museum, Pretoria.
- Patzkowsky, M. E. 2017. Origin and evolution of regional biotas: a deep-time perspective. *Annual Review of Earth and Planetary Sciences* 45:471–495.

- Peters, S. E., D. P. Quinn, J. M. Husson, and R. R. Gaines. 2022. Macrostratigraphy: insights into cyclic and secular evolution of the Earth-life system. *Annual Review of Earth and Planetary Sciences* 50:419–449.
- Pfennig, D. W., and K. S. Pfennig. 2012. *Evolution's wedge: competition and the origins of diversity*. University of California Press, Berkeley.
- Plotnick, R. E., and J. J. Sepkoski. 2001. A multiplicative multifractal model of originations and extinctions. *Paleobiology* 27:126–139.
- Prevosti, F. J., A. Forasiepi, and N. Zimicz. 2013. The evolution of the Cenozoic terrestrial mammalian predator guild in South America: competition or replacement? *Journal of Mammalian Evolution* 20:3–21.
- Prum, R. O. 2017. *The evolution of beauty: how Darwin's forgotten theory of mate choice shapes the animal world—and us*. Doubleday, New York.
- Queller, D. C. 2000. Relatedness and the fraternal major transitions. *Philosophical Transactions of the Royal Society of London B* 355:1647–1655.
- Radzevičius, S., A. Spiridonov, A. Brazauskas, D. Dankina, A. Rimkus, G. Bičkauskas, D. Kaminskas, T. Meidla, and L. Ainsaar. 2016. Integrated stratigraphy, conodont turnover and paleoenvironments of the Upper Wenlock and Ludlow of the Vilkaviškis-134 core (Lithuania). *Newsletters on Stratigraphy* 49:321–336.
- Rahbek, C., M. K. Borregaard, A. Antonelli, R. K. Colwell, B. G. Holt, D. Nogues-Bravo, C. M. Ø. Rasmussen, K. Richardson, M. T. Rosing, and R. J. Whittaker. 2019. Building mountain biodiversity: geological and evolutionary processes. *Science* 365:1114–1119.
- Ramsey, G., and C. H. E. Pence. 2016. *Chance in evolution*. University of Chicago Press, Chicago.
- Raup, D. M. 1991. A kill curve for Phanerozoic marine species. *Paleobiology* 17:37–48.
- Raup, D. 1992. *Extinction: bad genes or bad luck?* Norton, New York.
- Raup, D. M. 1994. The role of extinction in evolution. *Proceedings of the National Academy of Sciences USA* 91:6758–6763.
- Raup, D., and S. J. Gould. 1974. Stochastic simulation and evolution of morphology—towards a nomothetic paleontology. *Systematic Biology* 23:305–322.
- Raup, D., and J. Sepkoski. 1982. Mass extinctions in the marine fossil record. *Science* 215:1501–1503.
- Raup, D., and J. Sepkoski. 1984. Periodicity of extinctions in the geologic past. *Proceedings of the National Academy of Sciences USA* 81:801–805.
- Rebeck, C. A., A. M. Leroi, and A. Burt. 2011. Mitochondrial capture by a transmissible cancer. *Science* 331:303–303.
- Rinkevičiūtė, S., R. Stankevič, S. Radzevičius, T. Meidla, A. Garbaras, and A. Spiridonov. 2022. Dynamics of ostracod communities throughout the Mulde/lundgreni event: contrasting patterns of species richness and palaeo-community compositional change. *Journal of the Geological Society* 191: jgs2021–039.
- Rosenberg, M. 2022. *The dynamics of cultural evolution: the central role of purposive behaviors*. Springer Nature, Cham, Switzerland.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Roughgarden, J., S. F. Gilbert, E. Rosenberg, I. Zilber-Rosenberg, and E. A. Lloyd. 2018. Holobionts as units of selection and a model of their population dynamics and evolution. *Biological Theory* 13:44–65.
- Salazar-Ciudad, I., J. Jernvall, and S. A. Newman. 2003. Mechanisms of pattern formation in development and evolution. *Development* 130:2027–2037.
- Salthe, S. N. 1985. *Evolving hierarchical systems: their structure and representation*. Columbia University Press, New York.
- Salthe, S. N. 1991. Two forms of hierarchy theory in western discourses. *International Journal of General Systems* 18:251–264.
- Sánchez-Baracaldo, P., G. Bianchini, J. D. Wilson, and A. H. Knoll. 2022. Cyanobacteria and biogeochemical cycles through Earth history. *Trends in Microbiology* 30:143–157.
- Sander, P. M., and M. Clauss. 2008. Sauropod gigantism. *Science* 322:200–201.
- Sander, P. M., A. Christian, M. Clauss, R. Fehner, C. T. Gee, E.-M. Griebeler, H.-C. Gunga, J. Hummel, H. Mallison, and S. F. Perry. 2011. Biology of the sauropod dinosaurs: the evolution of gigantism. *Biological Reviews* 86:117–155.
- Schertzer, D., I. Tchiguirinskaia, S. Lovejoy, and P. Hubert. 2010. No monsters, no miracles: in nonlinear sciences hydrology is not an outlier! *Hydrological Sciences Journal/Journal des Sciences Hydrologiques* 55:965–979.
- Sears, K. E. 2004. Constraints on the morphological evolution of marsupial shoulder girdles. *Evolution* 58:2353–2370.
- Sepkoski, J. J., Jr. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7:36–53.
- Sepkoski, J. J. 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* 10:246–267.
- Shine, R., G. Brown, and B. Phillips. 2011. An evolutionary process that assembles phenotypes through space rather than through time. *Proceedings of the National Academy of Sciences USA* 108:5708–5711.
- Silver, D., J. Schrittwieser, K. Simonyan, I. Antonoglou, A. Huang, A. Guez, T. Hubert, et al. 2017. Mastering the game of Go without human knowledge. *Nature* 550:354–359.
- Simpson, G. G. 1983. *Splendid isolation: the curious history of South American mammals*. Yale University Press, New Haven, Conn.
- Simpson, C. 2011. The evolutionary history of division of labour. *Proceedings of the Royal Society of London B* 279:116–121.
- Solé, R. 2022. Revisiting Leigh Van Valen's "A New Evolutionary Law"(1973). *Biological Theory* 17:120–125.
- Sornette, D., and V. Pisarenko. 2003. Fractal plate tectonics. *Geophysical Research Letters* 30. <https://doi.org/10.1029/2002GL015043>.
- Spencer, C. J., N. S. Davies, T. M. Gernon, X. Wang, W. J. McMahon, T. R. I. Morrell, T. Hincks, P. K. Pufahl, A. Brasier, and M. Seraine. 2022. Composition of continental crust altered by the emergence of land plants. *Nature Geoscience* 15:735–740.
- Spiridonov, A. 2017. Recurrence and cross recurrence plots reveal the onset of the Mulde Event (Silurian) in the abundance data for Baltic conodonts. *Journal of Geology* 125:381–398.
- Spiridonov, A., L. Balakauskas, and S. Lovejoy. 2022. Longitudinal expansion fitness of brachiopod genera controlled by the Wilson cycle. *Global and Planetary Change* 216:103926.
- Spiridonov, A., and S. Lovejoy. 2023. Scaling in the evolution of biodiversity. *Biological Theory* 18:1–6.
- Spiridonov, A., A. Brazauskas, and S. Radzevičius. 2015. The role of temporal abundance structure and habitat preferences in the survival of conodonts during the mid-early Silurian Ireviken mass extinction event. *PLoS ONE* 10: e0124146.
- Spiridonov, A., A. Brazauskas, and S. Radzevičius. 2016. Dynamics of abundance of the mid- to late Pridoli conodonts from the eastern part of the Silurian Baltic Basin: multifractals, state shifts, and oscillations. *American Journal of Science* 316:363–400.
- Spiridonov, A., D. Kaminskas, A. Brazauskas, and S. Radzevičius. 2017a. Time hierarchical analysis of the conodont paleocommunities and environmental change before and during the onset of the lower Silurian Mulde bioevent—a preliminary report. *Global and Planetary Change* 157:153–164.
- Spiridonov, A., R. Stankevič, T. Gečas, T. Šilinskas, A. Brazauskas, T. Meidla, L. Ainsaar, P. Musteikis, and S. Radzevičius. 2017b. Integrated record of Ludlow (Upper Silurian) oceanic geobioevents—coordination of changes in conodont, and brachiopod faunas, and stable isotopes. *Gondwana Research* 51:272–288.
- Spiridonov, A., A. Venckutė-Aleksienė, and S. Radzevičius. 2017c. Cyst size trends in the genus *Leiosphaeridia* across the Mulde (lower Silurian) biogeochemical event. *Bulletin of Geosciences* 92:391–404.
- Spiridonov, A., J. Samsonė, A. Brazauskas, R. Stankevič, T. Meidla, L. Ainsaar, and S. Radzevičius. 2020a. Quantifying the community turnover of the uppermost Wenlock and Ludlow (Silurian) conodonts in the Baltic Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology* 549:109128.
- Spiridonov, A., R. Stankevič, T. Gečas, A. Brazauskas, D. Kaminskas, P. Musteikis, T. Kaveckas, et al. 2020b. Ultra-high resolution multivariate record and multiscale causal analysis of Pridoli (late Silurian): implications for global stratigraphy, turnover events, and climate-biota interactions. *Gondwana Research* 86:222–249.
- Spiridonov, A., and S. Lovejoy. 2022. Life rather than climate influences diversity at scales greater than 40 million years. *Nature* 607:307–312.
- Stanley, S. M. 1975. A theory of evolution above the species level. *Proceedings of the National Academy of Sciences USA* 72:646–650.
- Stanley, S. M. 1979. *Macroevolution: pattern and process*. Freeman, San Francisco.

- Stanley, S. M. 1990. *The general correlation between rate of speciation and rate of extinction: fortuitous causal linkages*. University of Chicago Press, Chicago.
- Stanley, S. M. 2008. Predation defeats competition on the seafloor. *Paleobiology* 34:1–21.
- Stern, R. J. 2023. The Orosirian (1800–2050 Ma) plate tectonic episode: key for reconstructing the Proterozoic tectonic record. *Geoscience Frontiers* 14:101553.
- Stigall, A. L. 2015. Speciation: expanding the role of biogeography and niche breadth in macroevolutionary theory. Pp. 301–327 in E. Serrelli and N. Gontier, eds. *Macroevolution* (Interdisciplinary Evolution Research 2). Springer, Cham, Switzerland.
- Stigall, A. L. 2019. The invasion hierarchy: ecological and evolutionary consequences of invasions in the fossil record. *Annual Review of Ecology, Evolution, and Systematics* 50:355–380.
- Stigall, A. L., J. E. Bauer, A. R. Lam, and D. F. Wright. 2017. Biotic immigration events, speciation, and the accumulation of biodiversity in the fossil record. *Global and Planetary Change* 148:242–257.
- Stigall, A. L., C. T. Edwards, R. L. Freeman, and C. M. Ø. Rasmussen. 2019. Coordinated biotic and abiotic change during the Great Ordovician Biodiversification Event: Darriwilian assembly of early Paleozoic building blocks. *Palaeogeography, Palaeoclimatology, Palaeoecology* 530:249–270.
- Stokes, M. F., D. Kim, S. F. Gallen, E. Benavides, B. P. Keck, J. Wood, S. L. Goldberg, I. J. Larsen, J. M. Mollish, and J. W. Simmons. 2023. Erosion of heterogeneous rock drives diversification of Appalachian fishes. *Science* 380:855–859.
- Szathmáry, E. 2015. Toward major evolutionary transitions theory 2.0. *Proceedings of the National Academy of Sciences USA* 112:10104–10111.
- Szathmáry, E., and J. M. Smith. 1997. From replicators to reproducers: the first major transitions leading to life. *Journal of Theoretical Biology* 187:555–571.
- Takeuchi, N., and K. Kaneko. 2019. The origin of the central dogma through conflicting multilevel selection. *Proceedings of the Royal Society of London B* 286:20191359.
- Tëmkin, I. 2021. Phenomenological levels in biological and cultural evolution. Pp. 297–316 in D. S. Brooks, J. DiFrisco, and W. Wimsatt, eds. *Levels of organization in the biological sciences*. MIT Press, Cambridge, Mass.
- Tëmkin, I., and N. Eldredge. 2007. Phylogenetics and material cultural evolution. *Current Anthropology* 48:146–154.
- Tëmkin, I., and N. Eldredge. 2015. Networks and hierarchies: approaching complexity in evolutionary theory. Pp. 183–226 in E. Serrelli, and N. Gontier, eds. *Macroevolution: explanation, interpretation and evidence* (Interdisciplinary Evolution Research). Springer, Heidelberg.
- Thompson, J. N. 2013. *Relentless evolution*. University of Chicago Press, Chicago.
- Tomašových, A., and S. M. Kidwell. 2010. The effects of temporal resolution on species turnover and on testing metacommunity models. *American Naturalist* 175:587–606.
- Torsvik, T. H., and L. R. M. Cocks. 2016. *Earth history and palaeogeography*. Cambridge University Press, Cambridge.
- Ung, V., and P. L. Buttigieg. 2023. BIOREALM—an ontology of comparative biogeography: new insights into the semantics of biodiversity conservation. *Journal of Biogeography* 50:1576–1586.
- Valentine, J. W., and E. M. Moores. 1970. Plate-tectonic regulation of faunal diversity and sea level: a model. *Nature* 228:657–659.
- Vanchurin, V., Y. I. Wolf, M. I. Katsnelson, and E. V. Koonin. 2022. Toward a theory of evolution as multilevel learning. *Proceedings of the National Academy of Sciences USA* 119:e2120037119.
- Van Dam, J. A., H. A. Aziz, M. Á. Á. Sierra, F. J. Hilgen, L. W. van den Hoek Ostende, L. J. Lourens, P. Mein, A. J. Van Der Meulen, and P. Pelaez-Campomanes. 2006. Long-period astronomical forcing of mammal turnover. *Nature* 443:687–691.
- Van Valen, L. 1973. A new evolutionary law. *Evolutionary Theory* 1:1–30.
- Van Valen, L. 1978. Why not to be a cladist. *Evolutionary Theory* 3:285–299.
- Van Valen, L. 1989. Three paradigms of evolution. *Evolutionary Theory* 9:1–18.
- Van Valen, L., and V. C. Maiorana. 1991. HeLa, a new microbial species. *Evolutionary Theory* 10:71–74.
- Van Valen, L. M. 1984. A resetting of Phanerozoic community evolution. *Nature* 307:50–52.
- Van Valen, L. M. 1991. Biotic evolution: a manifesto. *Evolutionary Theory* 10:1–13.
- Venckutė-Aleksienė, A., S. Radzevičius, and A. Spiridonov. 2016. Dynamics of phytoplankton in relation to the upper Homeric (lower Silurian) *lundgreni* event—an example from the eastern Baltic Basin (western Lithuania). *Marine Micropaleontology* 126:31–41.
- Vrba, E. S. 1980. Evolution, species and fossils: how does life evolve? *South African Journal of Science* 76:61–84.
- Vrba, E. S. 1985. Environment and evolution: alternative causes of the temporal distribution of evolutionary events. *South African Journal of Science* 81:229–236.
- Vrba, E. S. 1992. Mammals as a key to evolutionary theory. *Journal of Mammalogy* 73:1–28.
- Vrba, E. S. 1993. Turnover-pulses, the Red Queen, and related topics. *American Journal of Science* 293(A):418–452.
- Vrba, E. S., and N. Eldredge. 1984. Individuals, hierarchies and processes: towards a more complete evolutionary theory. *Paleobiology* 10:146–171.
- Vrba, E. S., and S. J. Gould. 1986. The hierarchical expansion of sorting and selection: sorting and selection cannot be equated. *Paleobiology* 12:217–228.
- Wagner, P. J., M. A. Kosnik, and S. Lidgard. 2006. Abundance distributions imply elevated complexity of post-Paleozoic marine ecosystems. *Science* 314:1289–1292.
- Walther, V., C. T. Hiley, D. Shibata, C. Swanton, P. E. Turner, and C. C. Maley. 2015. Can oncology recapitulate paleontology? Lessons from species extinctions. *Nature Reviews Clinical Oncology* 12:273–285.
- White, J. 1979. The plant as a metapopulation. *Annual Review of Ecology and Systematics* 10:109–145.
- Whittingham, M., S. Radzevičius, and A. Spiridonov. 2020. Moving towards a better understanding of iterative evolution: an example from the late Silurian Monograptidae (Graptolithina) of the Baltic Basin. *Palaeontology* 63:629–649.
- Wignall, P. B. 2015. *The worst of times: how life on Earth survived eighty million years of extinctions*. Princeton University Press, Princeton, N.J.
- Willis, J. C. 1922. *Age and area: a study in geographical distribution and origin of species*. Cambridge University Press, Cambridge.
- Wilson, E. O., and B. Hölldobler. 2005. Eusociality: origin and consequences. *Proceedings of the National Academy of Sciences USA* 102:13367–13371.
- Woodcock, N. H. 2004. Life span and fate of basins. *Geology* 32:685–688.
- Yablokov, A. V. 1986. *Phenetics: evolution, population, trait*. Columbia University Press, New York.
- Yacobucci, M. M. 2005. Multifractal and white noise evolutionary dynamics in Jurassic–Cretaceous Ammonoidea. *Geology* 33:97–100.
- Žliobaitė, I., and M. Fortelius. 2022. On calibrating the completometer for the mammalian fossil record. *Paleobiology* 48:1–11.
- zu Castell, W., U. Lüttge, and R. Matyssek. 2019. Gaia—a holobiont-like system emerging from interaction. Pp. 255–279 in L. Wegner and U. Lüttge, eds. *Emergence and modularity in life sciences*. Springer, Cham, Switzerland.