https://doi.org/10.15388/vu.thesis.887
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NATURE RESEARCH CENTER

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The HespDiv Method: Revealing the Hierarchical Organization of Biota in Space and Time

DOCTORAL DISSERTATION

Natural Sciences,
Geology (N 005)

VILNIUS 2026

The dissertation was prepared between 2020 and 2025 at Vilnius University.

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This doctoral dissertation will be defended in a public meeting of the Dissertation Defence Panel:

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The text of this dissertation can be accessed at the libraries of Nature Research Center and Vilnius University, as well as on the website of Vilnius University: www.vu.lt/lt/naujienos/ivykiu-kalendorius:
www.vu.lt/lt/naujienos/ivykiu-kalendorius

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VILNIAUS UNIVERSITETAS
GAMTOS TYRIMŲ CENTRAS

Liudas Daumantas

HespDiv metodas: biotos hierarchinės organizacijos laike ir erdvėje atskleidimas

DAKTARO DISERTACIJA

Gamtos mokslai,
Geologija (N 005)

VILNIUS 2026

Disertacija rengta 2020–2025 metais Vilniaus Universitete.

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Disertaciją galima peržiūrėti Vilniaus universiteto ir Gamtos tyrimų centro bibliotekose ir VU interneto svetainėje adresu:
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CONTENTS

INTRODUCTION

Actuality

This thesis addresses one of the most significant challenges in geobiological sciences and more recently biogeodynamics, which has intrigued us for centuries: explicating and understanding how the diversity of life is organized across space and time (Brown, 1995; Cox, 2016; Darwin, 1860; Wallace, 1876; Whittaker et al., 2013). Although many advancements have been made in this direction, each milestone achieved has opened up new avenues of important questions. The development and application of hierarchy theory (Koestler, 1967; Simon, 1962) to understand spatiotemporal organization of biological systems were very productive in this regard (Wu, 2011). It has been shown that genealogical entities of biota (e.g., organisms, species) exhibit temporal hierarchical organization (Eldredge, 1985), while ecological entities of biota (e.g., organisms, populations, communities, ecosystems) are also organized hierarchically, though mostly in space (Allen & Hoekstra, 2015; Allen & Starr, 2017; O'Neill, 1986).

The recognition that such biotic hierarchies exist called for the development of hierarchical methods to reveal and investigate these spatial and temporal hierarchical structures of biota organization. This call was met with a proliferation of various phylogenetic (Brooks & McLennan, 1991) and bioregionalization (Myers & Giller, 1988) methods. Recently, the frameworks of spatial and temporal biotic hierarchies were integrated with the hierarchical framework of geological structures, resulting in the so-called Bretskyan hierarchy (Spiridonov & Eldredge, 2024) – a spatiotemporal hierarchy of eco-genealogical polyphyletic entities named geobiomes (e.g., continent biota, island biota) and holobionts (e.g., multicellular polyphyletic superorganisms). This represents a new fundamental perspective on the spatiotemporal organization of biota across multiple scales.

The patterns of large-scale units within this Bretskyan hierarchy are a significant source of new macroecological and macroevolutionary information. They can provide crucial context in explaining and even predicting the spatiotemporal dynamics of macroevolution, macroecology, and biota organization in general. Considering the devastating, large-scale, and abrupt nature of current anthropogenic biotic and climatic turnovers (Barnosky et al., 2011; Intergovernmental Panel on Climate, 2023; Steffen et al., 2015), and the uncertainty surrounding their ultimate resolution and impact (Scheffer et al., 2001; Tollefson, 2020), such new fundamental theoretical developments in biotic hierarchy theory are critically needed. As with previous developments in biotic hierarchies, these new insights call for methodological developments and empirical applications to harness the full potential of the theory. However, partly due to the novelty of the Bretskyan hierarchy framework, no methods have been designed to distinguish hierarchies of Bretskyan units, rendering them "the Dark Matter of living systems" (Daumantas & Spiridonov, 2023) (Niles Eldredge, pers. comm.).

Thesis Goal:

Develop a methodological framework and methods for the effective analysis of hierarchical biota organization in space and time.

Thesis Tasks:

1. Review the literature of empirical and theoretical studies to understand the features of temporal and spatial organization of biota and the theoretical frameworks commonly applied in examining it.
2. Review the methods currently available for studying the spatiotemporal hierarchy of biota.
3. Develop an effective methodological framework that explicitly aligns with the Bretskyan hierarchy theory.
4. Develop computational algorithms in accordance with this methodological framework.
5. Integrate these methods into the widely available, open-source platform for statistical computation, namely R, as a package.
6. Validate the effectiveness of the approach by conducting case studies with empirical data of Silurian and Miocene biota.

Novelty and Significance

Recognizing the absence of suitable methods for Bretskyan hierarchy empirical studies, the new methodological framework was proposed named hierarchical spatial data subdivision (HespDiv), along with its two methods, which are available in the R package "hespdiv." HespDiv, among its other capabilities, has the capacity to reveal and characterise the units of the Bretskyan hierarchy. This will be demonstrated through two case studies where the developed methods were applied.

The first case study will demonstrate the HespDiv method *hespdiv* and its application to Miocene mammal fossil occurrence data from the contiguous United States to reveal its palaeobiogeography within the framework of Bretskyan hierarchy (Daumantas & Spiridonov, 2024b). This method hierarchically subdivides geographical space into contiguous clusters based on differences between fossil assemblages. Thus, the results obtained with *hespdiv* can be viewed as representing spatially resolved units of the Brestkyan hierarchy (i.e., a spatial cross-section through spatiotemporal hierarchy)

The second case study will demonstrate another HespDiv method – *birese* (binary recursive segmentation). Like the *hespdiv* method, *birese* is designed to subdivide data based on differences between fossil assemblages, but it does so across one dimension only (e.g., spatial transect, chronology, stratigraphy). This HespDiv method is explicitly Bretskyan in nature because its results can be interpreted to represent a temporal cross-section through Bretskyan units.

The relevance of the *birese* method is underscored by the fact that well-resolved spatial fossil data are much less common and harder and more expensive to obtain than high-quality fossil data from a single locality (e.g., core, outcrop) (for an overview of problems inherent to spatial fossil databases, see Antell et al., 2024). Here, also presented is the application of this one-dimensional HespDiv method to Silurian benthic ostracod species taxonomic composition and the abundance data from the Gėluva-118 core interval, which spans the Mulde/lundgreni biotic event horizons (Rinkevičiūtė et al., 2025).

This thesis thus establishes the first efficient and automated framework for separating spatiotemporal units of the Bretskyan hierarchy. This achievement was enabled by the development of the "holy triad" of the (1) methodological HespDiv framework, (2) its two methods (*hespdiv* and *birese*), and (3) their software, as well as the application of this triad to the empirical data of Silurian and Miocene biota. The significance of this achievement is that it demonstrates that the units of the Bretskyan hierarchy are not merely theoretical constructs, but can, in principle as well as in practice, be distinguished using the methods proposed in this work. Given this newly established ability, the methods developed and proposed in the thesis open up many new possibilities to extract and investigate various patterns of large-scale Bretskyan hierarchy units, their evolution, and the spatiotemporal organization of biota in general.

The case studies validating the effectiveness of the HespDiv framework and methods delivered scientifically interesting and novel results, in addition to the validation, demonstration, and characterization of the proposed quantitative approach.

The case study investigating the hierarchical structure of Miocene mammal occurrence data from the contiguous United States quantitatively delineated three major geobiomes (West Coast, Central Plains, and Southeast) for the first time. The shape of these geobiomes were closely related to the palaeogeography of the Miocene (Daumantas & Spiridonov, 2024b). There were also many correspondences between the bioregionalization schemes obtained and those established previously by other authors, validating the effectiveness of the HespDiv approach. Thus, the quantitatively identified geobiomes can be used as territorial sampling units in future studies of US Miocene mammals (e.g., in comparative studies that require fossil samples from distinct geobiomes).

Moreover, the results demonstrated that the Bretskyan units identified, along with the corresponding bioregionalization schemes, are fuzzy in nature. This is a significant finding as it confirms the prediction of Bretskyan hierarchy theory (Spiridonov & Eldredge, 2024), indicating that we should consider geobiomes (especially those smaller than a continent) and their spatiotemporal boundaries in probabilistic terms and use probabilistic methods for their identification. Very few other methods are suitable for bioregionalization (let alone Bretskyan bioregionalization) that provide means to evaluate this fuzziness and the statistical significance of distinguished bioregions and their boundaries. Meanwhile, the HespDiv family methods available within the "hespdiv" package are among the first designed explicitly for handling such uncertainties by permitting automated bioregionalization and its sensitivity analyses.

Applying *birese* to the Silurian (Homerian) ostracod abundance dataset obtained from the Gėluva-118 core, within which the Mulde/lundgreni event was previously localized and analysed using lower-resolution ostracod data (Rinkevičiūtė et al., 2022), produced a first-of-its-kind temporal cross-section of benthic ostracod Bretskyan hierarchy units (Rinkevičiūtė et al., 2025). This cross-section allowed for the quantitative and hierarchical framing of stratigraphical changes in fossil assemblages and the determination of the biostratigraphic boundaries of the Mulde/lundgreni event, as well as the boundaries of its internal stages.

Based on these biostratigraphic boundaries, for the first time, the duration and speed of this Homerian "Big Crisis" event were quantitatively estimated using a Bayesian age-depth model. The results showed that the Mulde/lundgreni biotic turnover event was likely shorter by an order of magnitude than previously estimated using semi-quantitative techniques (260 Ka vs. ~1 Ma) (Cramer et al., 2012). Such durations are comparable to the durations of Pleistocene glacial-interglacial cycles of 100 Ka (Hughes & Gibbard, 2018), suggesting the possibility of similar causal mechanisms.

Additionally, this study revealed an interesting pattern of two distinct, relatively long-lasting, stable diversity states, punctuated by a "mass rarity" phase during the peak of the "Big Crisis" event. This pattern aligns with the macroevolutionary dynamics predicted by the "coordinated stasis"(Brett, 2012), “punctuated equilibria” (Eldredge, 2024; Eldredge & Gould, 1972), and “sloshing-bucket” (Eldredge, 2003) hypotheses. This alignment demonstrates that the *birese* method can be a valuable tool in testing important hypotheses of macroevolution.

The HespDiv methodological approach, methods, and software were created with flexibility and generality in mind. They were designed to analyse many types and structures of data, whether palaeontological or otherwise. In both HespDiv methods, the input data can be hierarchically subdivided according to almost any kind of logic. The methodology and software not only allow users to choose from available pre-programmed subdivision methods but also to provide an R function as input to define a custom subdivision method. Additionally, HespDiv methods allow manipulation of multiple subdivision criteria, such as minimum area sizes, minimum number of observations, localities, and more. The combination of these flexibility and generality-enhancing features grants a formidable range of possible HespDiv applications to study the spatiotemporal organisation of biota, and beyond. Thus, the significance and novelty of the HespDiv approach also lie in this untapped potential.

Finally, this thesis makes several theoretical contributions. First, by methodological innovations and case studies it advances Bretskyan hierarchy theory by transforming it from a largely conceptual model into an empirically grounded and practically applicable framework for understanding the hierarchical organisation of biota in space and time. It also advances the theory by integrating concepts from complexity science—such as dissipative systems, energy gradients, and cross-scale coupling—thereby situating Bretskyan hierarchy theory within a broader framework of topologically related, nested, patch-based, dynamic hierarchies. This thesis establishes a strong connection between Bretskyan hierarchy theory and empirical palaeobiological research by demonstrating when, how, and with what degree of reliability geobiomes can be reconstructed from fossil data. It introduces a formal distinction between empirical, compositional hierarchies of bioregions (Bretskyan-like hierarchies)—characterised as nested, static, diachronic, and data-driven—and the ontological, dynamic, nested, anastomosing, compositional and control Bretskyan hierarchy of geobiomes. Additionally, the thesis expands the theory by proposing that large-scale geobiomes—particularly those associated with ecologically distinct habitat types—may spatially overlap, capturing the inherently complex and multiscalar structure of biotic organisation.

Theses:

- HespDiv is an effective, novel, foundational, and broad methodological approach, suited for the analysis of Bretskyan hierarchy units and constituting a new family of methods.
- The developed HespDiv methods (*hespdiv* and *birese*) not only help identify Bretskyan hierarchy units but can also provide new empirical insights into the spatiotemporal dynamics of biota.

1. THE TEMPORAL AND SPATIAL ORGANIZATION OF LIFE ON EARTH

This chapter of the thesis provides an overview of the theoretical foundations underlying the organisation of biota in space and time. It aims to bridge the gap between theory and application by highlighting key concepts relevant for evaluating methodological approaches presented later and interpreting the results of empirical case studies. Second chapter of the thesis also embodies the first task of the thesis (see Introduction).

1.1. Structural Complexity in Nature

As observers, we can perceive a wide variety of physical entities (e.g. atoms, molecules, minerals, cells, rocks, planetary bodies, organisms) interconnected through intricate cross-scale relationships and processes, forming complex systems that give rise to apparent order—not only within living and inorganic systems in our immediate surroundings, but also across broader cosmological scales. In the context of this thesis, this form of complex organisation is referred to as structural complexity. While particularly widespread in the biosphere, structural complexity is also evident in many abiotic systems. Accordingly, the principles governing its emergence are assumed to be universal, applying to both living and non-living systems. Thus, before exploring peculiars that apply to biosphere organisation it is a must to explore the universals that organise both biota and abiota. This section provides an overview of these underlying principles.

1.1.1. Perplexing Emergence of Structural Complexity

Since the singularity, the number and diversity of physical entities—such as stars, galaxies, planets, and life—have continuously increased (Chaisson, 2001). This may appear counterintuitive, given that the universe's entropy—

defined as the number of microstates accommodated by a given macrostate, or more simply, as a measure of disorder—is continually increasing over time, thereby defining the arrow of time (Carroll, 2016). More strikingly, this structural complexity and diversity are highly unequally distributed in both space and time. However, advances in cosmology, natural sciences, non-equilibrium thermodynamics, systems theory, hierarchy theory, and complexity science have provided insights into the underlying principles that generate order, helping to resolve this apparent paradox of simultaneous entropy increase and growing structural complexity, as well as their heterogeneous spatial distribution (Ahl & Allen, 1996; Carroll, 2016; Chaisson, 2001; Prigogine, 1984; Salthe, 1985; Simon, 1962).

1.1.2. Dissipative Systems and Gradient-Driven Change

To understand how order arises under non-equilibrium conditions, the concepts of dissipative systems and dissipative structures are fundamental (Prigogine, 1984; Prigogine & Nicolis, 1971). In non-equilibrium thermodynamics, dissipative structures are ordered systems whose self-organisation is maintained through continuous flows of energy or matter—flows driven by energy gradients (i.e. spatial differences in thermal, gravitational, chemical, or other forms of energy, representing the potential for energy flow). These structures operate far from thermodynamic equilibrium and dissipate energy in the process. A broader concept is that of dissipative systems, which similarly depend upon sustained flows of energy or matter and operate far from equilibrium, dissipating energy, but do not necessarily display self-organisation or emergent order. By definition, all dissipative structures are a subset of dissipative systems. Dissipative structures are significant in this context as they represent physical entities that produce new energy gradients by dissipating existing ones.

Beyond dissipative structures, there also exist ordered yet non-dissipative structures—such as crystal lattices, galaxies, and planets—which emerge due to energy gradients, often within or as a consequence of dissipative systems. These structures dissipate energy much less actively and do not require ongoing energy flows to persist. Consequently, they can persist for long durations and may generate new energy gradients if they later interact with other structures or gradients (e.g. a meteorite colliding with Earth and becoming integrated into its systems).

1.1.3. Physical Entities and the Cascade of Gradient Formation

The interaction of physical entities (e.g. electrons, atoms, molecules, planets, organisms, fields, various dissipative and non-dissipative structures) with energy gradients underpins the emergence of structural complexity in the universe (Chaisson, 2001; Prigogine, 1984) and is best understood in terms of non-equilibrium thermodynamics. The universe began in a highly ordered, low-entropy, non-equilibrium state, and this condition enabled the Second Law of Thermodynamics to take effect, initiating a prolonged and perhaps even endless evolution towards equilibrium. According to this law, entropy increases across the universe, primarily facilitated by the dissipation of energy gradients, which drive irreversible processes and expand the number of accessible microstates per macroscopic state. Energy gradients and their dissipation are inseparable from the physical systems in which they occur (Prigogine, 1984). Consequently, energy gradients necessarily involve some physical entity and their dissipation is fundamentally driven by the interaction with physical entities.

Energy gradients and the physical entities on which they depend are finite and typically short-lived. This raises an apparent paradox: if individual gradients dissipate, why does motion and change across the universe persist? The persistence of structural complexity and of multiple active gradients implies that certain physical laws and mechanisms continually generate cascades of new gradients and entities. Scaling is crucial to this continuity: large, long-lived gradients provide the conditions under which smaller, short-lived gradients can emerge. Moreover, the unequal distribution of structural complexity across space and time suggests that the cascade process is probabilistic and inhomogeneous, with regions such as Earth representing statistical extremes.

Biological diversity offers an analogous case: evolutionary radiations and mass extinctions highlight how complexity can wax and wane. New physical entities—such as the global network of technological civilisations formed by a single species, Homo sapiens—have the capacity to either increase or diminish the overall structural complexity of the biosphere. This is evidenced by anthropogenic climate change, biodiversity loss, and the widespread transformation of natural landscapes through human activity. In this sense, the evolution of the universe can be viewed as a cascading stochastic sequence of formation and dissipation of scaling energy gradients and physical entities. This sequence may locally or temporarily stagnate or truncate if no new gradients emerge, or if existing conditions dissipate energy gradients at a rate equal to or exceeding the rate at which new ones are generated.

1.1.4. Two Principles of Gradient-Entity Interaction

Two main principles help explain how the cascading formation of energy gradients sustains spatially and temporally heterogeneous structural complexity:

1. *The relationship between physical entities and energy gradients*: Physical laws, along with interactions among physical entities can lead to the creation, amplification, reduction, or destruction of energy gradients. The outcome depends on the properties of the entities and the configuration of the gradients.
2. *Energy gradients as agents of transformation:* Energy gradients affect the motion and properties of physical entities, sometimes fostering self-organisation and the emergence of new entities, and at other times causing disintegration. The specific effects are determined by the nature and spatial configuration of both the gradients and the interacting entities.

Together, these principles imply that energy gradients can give rise to further gradients through their effects on physical entities, and that physical entities can generate new entities via gradient-mediated interactions. Processes such as sediment sorting by water flow, fractional crystallisation of magma, or differential weathering of rocks illustrate how the differential responses of physical entities to energy gradients can result in the emergence of new spatial arrangements of existing matter, and combination into entirely new physical entities. Likewise, the convergence of two tectonic plates and the consequent uplift of mountain ranges—creating a gravitational potential gradient—drives the development of features such as rivers, glacial valleys, and deliuvium cones, which act to dissipate this gradient. This exemplifies how physical entities, themselves driven by energy gradients, can initiate a cascade of new gradients that in turn foster the emergence of further physical structures.

1.1.5. Persistence of Physical Entities

The persistence of physical entities is essential for both the continuous generation and dissipation of energy gradients and for maintaining the structural integrity of larger systems composed of smaller entities. Together, these dynamics underpin the emergence and long-term maintenance of structural complexity. At least three primary modes of persistence can be distinguished (Simon, 1962; Spiridonov & Eldredge, 2024; Wu & Loucks, 1995):

1. *Durability*: The simplest form of persistence. More durable entities—such as atoms, minerals, rocky bodies, planets, or trees—persist over long timescales and are more likely to accumulate or serve as stable building blocks for other physical entities. Various factors determine durability and, by extension, persistence: homeostasis (the ability to maintain internal conditions conducive to survival despite external perturbations), homeorhesis (the ability to retain a developmental trajectory despite disturbances), the capacity to cycle internal components, and strong rheological structural integrity.
2. *Replication / Fabrication:* Entities that replicate or are continually fabricated at a rate exceeding their destruction can accumulate and contribute to more complex, metastable structures (e.g. populations, communities) (Wu & Loucks, 1995). In biological systems, this occurs via self-replication (e.g. cell division). In abiotic systems, analogous persistence arises through cyclical, iterative, or recursive processes driven by existing gradients and entities (i.e. "fabrication"). Examples include sand production through weathering, lithological renewal via mantle convection and tectonics, and biogeochemical cycling of chemical elements. Recursive processes—such as stalactite growth, sediment layering, dune rolling, or stream incision—sustain fractal-like structures over extended periods (Milne, 1991), supporting dependent entities like riverine ecosystems.
3. *Redundancy / Interchangeability / Availability of Components:* physical entities that continuously cycle their composition depend on their availability. Also, any spontaneous emergence of new physical entity depends on component availability in the environment. Redundancy can also emerge from functional overlap of physical entities that act as components of other physical entities (degeneracy). In ecosystems, multiple species may fulfil similar roles. In neural systems, degeneracy allows different neurons to perform overlapping functions. Similarly, mineralogically different sand grains on a beach can maintain its emergent properties despite continual turnover. Different trees can shape forest. Thus, durability, replication / fabrication rate and degeneracy all contribute to redundancy and availability.

1.1.6. Nested Complexity and Contingency on Low-Probability Conditions

The presented framework also explains the patchy distribution of structural complexity. Regions already rich in mass and diverse physical entities, as well as gradients are statistically more likely to generate new gradients and entities. Yet, complex systems like Earth with the complex life it supports are rare among planets (Ward & Brownlee, 2004), likely requiring specific initial conditions and low-probability events with the right timing along their evolution (e.g. the hypothesised collision with Theia that formed the Moon and altered planet's composition (Canup & Asphaug, 2001; Ćuk & Stewart, 2012; Elkins-Tanton et al., 2011)) that push them far from their thermodynamic equilibrium.

Under these rare conditions, cross-scale interactions between energy gradients and physical entities are likely one of the main mechanisms that sustain cycling of physical entities and energy gradients. Newly formed entities often create localised secondary gradients, which in turn support additional entities at smaller scales. Conversely, smaller-scale entities may combine into larger systems. Under suitable conditions, even weak energy gradients and entities can interact meaningfully—as evidenced by human ability to observe and thus respond (using fabricated instruments) to small seismic vibrations, gravitational waves, or collisions of elementary particles. Consequently, planets like Earth can become densely populated with nested gradients and interconnected physical entities operating at multiple scales.

1.1.7. Spatial Coupling of Energy Gradients

The spatial intersection and coupling of source-distinct yet co-located energy gradients are one more crucial factor in generating multi-level, spatially and temporally organised structural complexity and in directing energy flow across scales. On planets like Earth, which contain internal dissipative systems, gradients generated internally can interact with solar radiation gradients, producing a nested cascade of gradient-driven processes and structures (Lovejoy & Schertzer, 2013).

The earliest mass–energy fluctuations, rooted in quantum foam and cosmic inflation (Baumann, 2009; Mukhanov & Chibisov, 1981), seeded gravitational potential wells that formed galaxies and galaxy clusters. Within them, the gravitational collapse of dust clouds triggered by potential gradients gave rise to distinct ordered, high-entropy structures—stars and planets. Stars are dissipative structures and thus support production of energy gradients and physical entities; planets, by contrast, are typically non-dissipative, but can support some gradients and physical entities solely due to external influences (e.g. stellar radiation and meteorite impacts).

Stellar radiation, when differentially absorbed by a planet's surface and atmosphere, establishes large-scale thermal and pressure gradients. These drive global dissipative systems such as atmospheric convection and ocean circulation (Basalykas, 2008), which in turn sustain secondary gradients (e.g. in salinity, humidity, electrical potential, and localised temperature or pressure). These gradients support smaller-scale dissipative structures such as weather systems, storm fronts, and oceanic upwelling zones (Lovejoy & Schertzer, 2013). Together, these features interact not only among themselves but also with gradients produced by the planet's interior.

During planetary formation, gravitational potential gradients drove the accretion of matter, increasing internal pressure and generating geothermal gradients through compressional heating and radioactive decay. This enabled partial melting and the chemical differentiation of Earth's internal layers, leading to stratified chemical, thermal, mechanical (rigidity), and magnetic gradients (Elkins-Tanton, 2012; Turcotte & Schubert, 2014). These, in turn, later supported large-scale dissipative systems like mantle convection and plate tectonics, which maintain and recycle Earth's internal and surface structures—including tectonic boundaries, mountain ranges, mantle plumes, and surface-level variations in topography, mineralogy, and geochemistry.

The existence of the Moon also sustains diverse gravitational gradients across the globe and influences nutrient, moisture, and other environmental gradients in tidal zones. Such dynamics were likely important for the terrestrialisation of land by animals as evidenced by transitional forms such as Tiktaalik roseae, which evolved in shallow, fluctuating freshwater environments that may have functioned similarly to tidal systems in shaping adaptations for life at the water–land interface (Daeschler et al., 2006).

The spatial intersection and subsequent coupling of solar, terrestrial (internal Earth), and lunar-driven energy gradients drive a nested cascade of increasingly complex structures and dynamic processes. This interaction gives rise to a wide variety of geological and environmental features—such as rivers, glacial landforms, lakes, deserts in rain shadow areas, volcanoes, and specialised environments including hydrothermal vents, tidal zones, and cave systems—each shaped by overlapping gradients.

In such diverse and dynamic settings, where various abiotic, transforming, and mobile dissipative systems coexist and interact across multiple scales with each other and with non-dissipative structures, a significant portion of the combinatorial space of physical and chemical conditions can be explored through chance alone (i.e. via random walk in a state space). The probability that such exploration results in conditions conducive to prebiotic chemistry and the origin of life is likely to be much higher than in less diverse and less dynamic settings characterised by much narrower state space—those lacking spatially overlapping energy gradients sustained by independent entities such as the Sun, Earth, and Moon. Thus, first principle reasoning suggests that the geodiversity is a key for the emergence of evolution and the cellular life from the earliest stages.

Once kick-started abiotically, the biosphere can be regarded as an emergent source of additional energy gradients and physical entities. In turn, it has further diversified Earth's surface, atmosphere, hydrosphere, and potentially even the geosphere (e.g. through altered geochemical cycles and the composition of subducted oceanic plates). Thus, the emergence of life brought about levels of variability and diversity on Earth that were previously unattainable. This aligns with earlier discussions: the added layer of structural complexity introduced by the spatial coupling of more diverse and abundant physical entities, along with more dynamic and overlapping energy gradients, acts to further propel the growth of structural complexity. It also increases system dynamics due to contingency—for example, certain states may be detrimental, leading to sharp declines in structural complexity.

To summarise, the spatial coupling of diverse and dynamic abiotic energy gradients and physical entities within pre-existing structural complexity underlies both the emergence and subsequent diversification of life, thereby accelerating and destabilising the structural complexity of the Earth system.

1.1.8. The Apparent Order of Patches and Smoothness, and Entities as Patches

The distribution of physical entities, energy gradients, their interactions, and associated changes in their characteristics over time and space is far from random—so much so that it allowed Waldo Tobler (Tobler, 1970) to formulate the first law of geography: "Everything is related to everything else, but near things are more related than distant things." This non-randomness manifests in several ways (these ideas overlap with hierarchical patch dynamics paradigm of Wu and Loucks (1995) applicable in landscape ecology context):

1) Variation in properties across spacetime is patchy, as if spacetime is divided into distinct regions (hereafter referred to as 'patches') with relatively uniform internal characteristics.
2) Variation in properties across spacetime is gradual, particularly within patches.
3) Variation in properties among patches is itself patchy, as smaller, similar patches aggregate into larger, spatially contiguous patches.
4) Variation in properties among patches is also gradual, as patches are typically more similar to adjacent patches.

Such structured variation not only allows us to regionalise spacetime (as practised in cartography, biogeography, and stratigraphy), but also facilitates predictions of unknown properties at nearby locations through geostatistical methods such as kriging (Davis, 2002).

The characteristics associated with the emergence of structural complexity explain how such ordered variation arises. Under idealised conditions (a single, temporarily stable energy source, absence of interfering gradients or entities, and a homogeneous medium), energy gradients appear smooth, which inherently promotes gradual property variations, particularly within homogeneous spacetime patches. However, spatial coupling of energy gradients with other gradients and physical entities can lead to spontaneous emergence of new entities. These entities dissipate the existing gradient to some extent, creating new patches even under relatively idealised conditions once a tipping point is reached. Physical state changes are particularly important emergent responses to smooth gradients. For example, a smooth thermal gradient can lead to the formation of ice patches when water is present, and temperatures fall below zero. Similarly, residual snow and ice patches persist in areas where temperatures remain sufficiently low, despite an overall warming trend.

Fractioning or sorting of physical entities provides another example where differential responses of various entities to the same smooth gradient can lead to the formation of self-similar patches, each distinct from others. As wind or water flow gradually reaches the threshold velocity required to mobilise, erode, or deposit otherwise stable material, this can result in the formation of new physical entities, such as geological layers with varying textures, erosion marks, dust storms, or ventifacts. Similarly, the fractionation of a melt during cooling—guided by crystallisation sequences—can produce distinct igneous rock layers, even in response to a smoothly declining thermal gradient.

These examples highlight the importance of conceptualising energy gradients not only in space but also in time. Smoothly dissipated or amplified gradients at a single location produce smooth temporal changes in energy (e.g. gravitational potential and associated water flow speed), which in turn influence the behaviour of physical entities that respond to them (e.g. through erosion or deposition). Such temporal gradients are observable in phenomena such as diurnal temperature cycles, tidal fluctuations, and seasonal variations in solar radiation. In geological systems, temporal gradients are exemplified by the gradual decline in particle size during sediment transport or the progressive accumulation or dissipation of geothermal heat. In biological systems, they manifest through processes such as circadian rhythms, population growth or decline, and the progressive accumulation or depletion of key resources within organisms (e.g. glucose, oxygen, fat) or ecosystems (e.g. primary producers, water).

Newly formed physical entities often couple and interact with co-located entities and gradients, disrupting otherwise smooth energy flows. This interference can lead to a cascade of spontaneous emergence or destruction of physical entities. For example, ice formation as a tipping point response to a smooth thermal gradient can abruptly alter the temporal gradient of water turbulence, resulting in the deposition of distinctly finer sediment particles and the formation of varved sedimentary sequences. Oxygen and nutrient gradients can guide invertebrate burrowers into varved sediments, where they dissipate their own chemical energy gradients while searching for food. This bioturbation results in the formation of new physical structures, altering the sediment's mechanical and chemical properties. The produced ichnofossils can affect processes such as water filtration rates and pathways, as well as diagenetic transformations like mineral dissolution and precipitation—ultimately leading to the emergence of even smaller-scale physical entities / patches (e.g. diagenetic minerals).

The example provided illustrates a downward progression from large to small patches, successively populating space with an increasing number of progressively smaller physical entities: from a non-turbulent, ice-covered lake, to varved sediment layers, to bioturbation structures, and ultimately to diagenetic minerals. However, this is not the only possible direction of progression. For example, the expansion of tree patches can generate forest patches; interacting populations of species within a shared habitat can give rise to an ecosystem-level patch; and similarly, individual bioturbations may aggregate into larger bioturbated sediment patches—potentially more suitable habitats for burrowers (and their consumers) due to altered redox conditions. Thus, the coupling of co-located physical entities and energy not only drives the cascade of new entities and gradients—even under conditions of smooth variability—but also does so in a patchy, ordered manner. This process generates a spatially organised hierarchy of patch mosaics, within which each patch may still exhibit relatively smooth internal variability (Wu & Loucks, 1995)

As the number and diversity of distinct physical entities increase, the spatiotemporal fabric of energy gradients becomes increasingly convoluted, producing more dynamic and heterogeneous environments. These environments, although structured in a patchy manner, retain gradual internal transitions. The interactions within such diverse environments can result in the flattening, amplifying, emergence, or convolution of energy gradients, along with the combination, recombination, disappearance and emergence of physical entities across multiple scales.

Each patch—defined by relatively uniform properties over a specific spatial or temporal scale—can be considered a physical entity. Correspondingly, an abrupt shift in an otherwise smooth energy gradient often signals a response to the presence of such an entity. Given their internal coherence, patches are likely to exhibit relatively synchronised and coherent responses to smooth external gradients (e.g. lake ice melting uniformly in response to warming temperatures). In contrast, steep, step-like or highly localised gradients can drive asynchronous, localised transformations, leading to the formation of smaller, nested patches—for instance, contact aureoles forming around igneous intrusions due to sharp thermal gradients; a step-like thermal gradient may form where lava flows over rock surfaces.

Similarly, convoluted gradients can partition previously uniform spacetime patches into more complex mosaics. For example, sand ripples act as convoluted gradients, modulating gravitational and wind-driven forces in ways that affect local sediment mobility and produce banded patterns of heavy mineral sorting.

Conversely, the disintegration of physical entities or their mixing can homogenise properties and eliminate patch boundaries, reducing structural complexity. In general, increasing structural complexity should be associated with a rise in the number and diversity of distinct patches or entities across a range of scales. This could be observed geostatistically as a decrease in spatial autocorrelation or an increase in spatial specificity of system behaviour. For example, the regional distribution patterns of prehistoric human settlements in Lithuania, from the Palaeolithic to the Late Iron Age, exhibit increasing statistical specificity in relation to regional environmental variables. This trend is reflected in the declining spatial autocorrelation of regional settlement probability maps and the growing superiority of predictive settlement location models over null models—both of which indicate increasing structural complexity in human populations, specifically in their settlement strategies, and a corresponding roughening of the human adaptive landscape (Daumantas et al., 2020). This transformation was likely driven by an increasingly diverse range of energy gradients and entities to which human populations responded and became dependent upon, as well as by the emergence of new entities within human populations (e.g. distinct settlement types) with distinct environmental preferences.

As energy gradients change at the boundaries of physical entities or patches and interactions tend to occur at these interfaces, this makes them the most transient and least stable structures within a mosaic of patches. All combinations of patch boundary and size interaction with energy gradient are possible, depending on the presence of positive, negative, or balanced feedback loops, and the diversity of entities and energy gradients involved:

- Gradient amplification through:
    - Shrinking (e.g. the spread of fire through the contraction of forest patches; energy is dissipated from the forest into the surrounding environment),
    - Retaining size (e.g. quartz sand amplifies thermal gradients without shrinking; while dissipating solar energy, it redistributes and concentrates it as heat),
    - Increasing in size (e.g. the spread of vegetation depends on moisture gradients, and vegetation expansion can in turn sustain or amplify these gradients; the primary gradient dissipated is solar radiation).
- Gradient dissipation through:
    - Shrinking (e.g. ice melts and shrinks while absorbing heat, thereby dissipating a thermal gradient),
    - Retaining size (e.g. living cells dissipate chemical energy to maintain their structure or grow),
    - Increasing in size (e.g. ice formation releases latent heat, thereby dissipating a thermal gradient while increasing in size).

Given the expectation that similar patches of entities will respond in similar ways to similar energy gradients, it is useful to categorise them based on similarity—treating them as members of the same class of entities. For example, we can reasonably expect all water to freeze if the temperature falls below 0 °C, to thaw if it rises above 0 °C, and to boil and evaporate if it exceeds 100 °C; no matter where, when, or in what conditions it is. Thus, it is meaningful to classify water as a consistent entity type. For many small-scale entities—such as individual atoms, molecules, or fine-grained material patches—this kind of similarity-based classification is sufficient, as their specific fates are relatively inconsequential within the broader system. However, as physical entities grow larger, persist longer, or become structurally or functionally significant within their environment, the knowledge of their individual fates become more meaningful. Their spatial context, specifically interactions with local entities and local gradients, are likely to direct their future behaviour in unique ways. As noted by (Spiridonov & Lovejoy, 2022): “If, for example, there are two ecologically similar clades on two isolated but in all respects equivalent continents (or marine basins), a change in the climate could produce very different carrying capacities. On the other hand, if both clades are in contact, the superior one will dominate, and a climate fluctuation will result in the same change in carrying capacities in both places". Thus, in such cases where fates of individuals are significant, it becomes necessary to treat each patch as distinct, context-dependent systems even if they are identical—requiring location-wise or interaction-based classification in addition to similarity-wise grouping.

All interactions between physical entities and energy gradients require spatial intersection. As a result, such interactions occur more frequently—and with greater immediacy—at closer spatial proximities, where they involve fewer intermediaries, shorter causal chains, and faster response times. The frequency of meaningful interactions over time is therefore expected to scale inversely with both spatial and temporal distance. For example, all marine organisms across the globe are likely to be integrated by causal links whose chain lengths are mostly less than ~40 Ma, contributing to: 1) the achieved global synchronisation and genealogical spatial mixing of biota at those temporal scales; 2) the dominance of diversity-driven macroevolutionary dynamics at those and larger temporal scales; and 3) a reduced ability to predict biotic dynamics from abiotic factors at those and larger temporal scales (Spiridonov & Lovejoy, 2022, 2023). However, interactions that rely on long causal chains tend to become unpredictable, as information is increasingly lost or transformed across intermediate steps. While all entities in the universe are ultimately causally connected, having originated from the same singularity, this foundational link provides no useful information about specific causal pathways in the present. As the universe continues to expand and diversify, causal chains lengthen, interactions grow more indirect, and some become effectively impossible due to distance. Consequently, predictive accuracy diminishes—particularly in complex, non-linear systems. This limitation is exemplified by the challenges of meteorological forecasting: although weather systems obey physical laws, their enormous complexity, sensitivity to initial conditions, and chaotic feedbacks severely constrain long-term predictive power.

Thus, close spatial and temporal proximity implies a distinct set of meaningful interactors, which in turn generates unique system dynamics over time. It follows that each patch will exhibit its own divergent history of patch transformations. Thus, entities classified according to both similarity and location- or interaction-based criteria are likely to evolve more coherently and to exhibit a higher degree of individuality—reflected, for instance, in the persistence of patch boundaries over time despite internal changes in properties, and cycling though different states.

To conclude, structural complexity and the patchy yet gradual variation of spacetime properties arise from local interactions among physical entities and energy gradients. These interactions give rise to spatiotemporally contiguous patches which, when classified by similarity and interaction dynamics, retain individual evolutionary trajectories and collectively form hierarchical, nested, causally integrated systems across scales. Identifying and studying such causally integrated systems is essential for understanding the emergence, organisation, and dynamics of complexity in natural systems.

1.1.9. Entropy, Order, and the Second Law

While this nested, cascading emergence of structure and patchy hierarchy may appear to contradict the Second Law of Thermodynamics, it in fact exemplifies it. Ordered non-dissipative structures are formed through processes that involve energy dissipation, whereas dissipative ordered structures persist through continuous energy dissipation. In both cases, the energy dissipated—and the associated increase in entropy in the surroundings—exceeds the local entropy reduction resulting from the formation or maintenance of the ordered structure (Prigogine, 1984). Thus, despite local decreases in entropy, the net entropy of any system and its environment always rises (e.g. in living systems; England, 2013). Therefore, ordered structures accelerate entropy production. Thereafter, structural complexity emerges not in spite of, but because of, the Second Law of Thermodynamics (Prigogine, 1984).

1.1.10. Summary

Structural complexity emerges through the interplay of physical entities and energy gradients, driven by their interactions under non-equilibrium conditions. These interactions not only dissipate existing gradients but also frequently generate new ones, along with new physical entities—producing cascading patterns of complexity. A key mechanism underlying this process is the spatial intersection and coupling of distinct gradients, which enables the formation of nested, spatiotemporally contiguous systems and accelerates entropy production across scales. Regions with a high spatial density of interactors—both gradients and entities—are statistically more likely to foster further interactions, thereby reinforcing and deepening structural complexity.

This emergent structure is not random. Instead, it appears as a mosaic of patches—regions of relative internal uniformity—characterised by gradual transitions and bounded by zones of steep gradient change. Each patch retains coherence in its responses to external gradients and thus follows an internally consistent evolutionary trajectory. As a result, patches can be seen as fundamental organisational units of complex systems. For small-scale entities (e.g. molecules or grains), similarity-based classification often suffices, but as entities grow larger and more consequential, their individual, context-dependent fates demand interaction- and location-based treatment. Interactions among patches and energy gradients drive both the emergence of new structures and the dissolution of existing ones, shaping the landscape of change across scales. This generates a patchy yet hierarchical spatial order in which each level contains embedded variation and interacts with levels above and below.

Cross-scale dynamics play a crucial role: smaller-scale interactions can give rise to larger-scale systems, while broader gradients constrain, generate, and are themselves reshaped by finer-scale structures. As new patches and gradients emerge, the spatiotemporal fabric of the system becomes increasingly convoluted—yielding more diverse, dynamic, and hierarchically structured environments. However, the emergence and maintenance of such complexity often depend on low-probability conditions and contingent events, which shape its uneven distribution in both space and time.

Equally critical is the persistence of physical entities, which ensures the continuity of gradient generation, dissipation, and structural integration across scales. Durable, replicating, or functionally redundant entities provide the material substrate for complex systems to emerge, stabilise, and evolve. Without such persistence, cascading interactions would collapse, and structural complexity could not be sustained over time.

Finally, because each patch emerges from unique interactions at specific spatial and temporal proximities, every location exhibits its own distinct history of patch transformation. Entities classified by both similarity and interaction dynamics retain higher individuality, preserving coherent trajectories despite shifting internal states. Thus, structural complexity arises through recursive, scale-bridging interactions that continuously generate, organise, and recycle energy gradients and entities—contingent on both statistical likelihood and rare, path-dependent evolutionary trajectories. Recognising and studying such causally integrated, patch-based systems is essential for understanding the emergence, organisation, and dynamics of complexity in the natural world.

1.2. Hierarchy Theory

The previous section should have provided a general idea of structural complexity of nature is, how widespread it is, how manifests itself, and how it may emerge. The next step is to frame this complexity in most efficient and clearest way. This is where hierarchy theory becomes handy. It is a general theory concerning the identification and organization of functional classes from observations (Allen, 2009), as well as understanding properties and emergence of hierarchical organizations (Corominas-Murtra et al., 2013; Simon, 1962). Note, that hierarchy theory is not a typical theory that offers some testable predictions itself (Wu, 2011) (on the other hand, it might, considering such studies as Corominas-Murtra, 2013). Instead, it guides the construction of efficient hierarchal theories specific to some fields of research and purposes. But in the end, it facilitates the production as testable hypothesis as constructed hierarchy theories can provide testable predictions (e.g. Spiridonov & Eldredge, 2024). Hierarchy theory is a highly interdisciplinary and theoretical framework. Most related fields would be complexity science and system theory.

Although various hierarchical approaches were used since ancient times (not necessarily these approaches were recognised as such then), the twentieth century is when the concept of hierarchy was firmly established in science. It was a recurrent theme with burst of interest manifesting in 1930s, 1960s and 1980s (Grene, 1987; O'Neill, 1986; Wu, 2011). The latter burst of theory culminated in body of literature defining and discussing various hierarchies (eg. Ahl & Allen, 1996; Allen & Hoekstra, 1992; Allen & Starr, 1982; Eldredge, 1985; Eldredge & Salthe, 1984; O'Neill, 1986; Salthe, 1985; Wu & Loucks, 1995) that constitute the basis of references in recent publications. Since 2000s new editions of these earlier contributions came out (e.g. Allen & Hoekstra, 2015; Allen & Starr, 2017) as well as a number of works discussing and applying existing hierarchy theories (e.g. Eldredge, 2008; Miller, 2008; Wu, 2011), as well as proposing new ones (e.g. Nakajima, 2004; Spiridonov & Eldredge, 2024). Thus, hierarchy theory is not entirely new, growing field of research.

A number of various hierarchy theories have been proposed since the inception of the field, and even before it (e.g. Carl Linneus established taxonomical hierarchy in 1762). There are numerous hierarchical approaches and well-established hierarchy theories in diverse array of fields like management (e.g. analytic hierarchy process within decision making theory (Saaty, 1980), hierarchy of authority), psychology (e.g. Maslow’s hierarchy of human needs (Kenrick et al., 2010)), geography (e.g. settlement hierarchy within central place theory (King, 1985)), cosmology (e.g. hierarchy of cosmic web and its properties (Jaber et al., 2023)), archaeology (typological and genealogical material culture hierarchies, site-size and regional political hierarchies (Duffy, 2015)), linguistics (e.g. genealogical and typological language family hierarchies), geology (various stratigraphic, geochronologic hierarchies, and hierarchies of geological, palaeogeographical, planetary structure bodies (Torsvik et al., 2019)), and they are particularly abundant in disciplines of biological sciences: ecosystem (Ahl & Allen, 1996; Allen & Hoekstra, 1992; Allen & Starr, 1982; O'Neill et al., 1986), community (for overviews of such hierarchies refer to (Salthe, 1985)), and landscape ecology (Wu & Loucks, 1995), taxonomy/systematics (Linnean hierarchy), biogeography (e.g. hierarchical classification of biota into spatial units such as realms, and biotic provinces are common since (Wallace, 1876)) and evolutionary biology (phylogenetic graphs represent information transmission and composition hierarchies; also – genealogical hierarchy (Eldredge, 1985; Eldredge & Salthe, 1984), dual hierarchy (Eldredge, 1985; Eldredge & Salthe, 1984), as well as hybrid (geo)biological hierarchies (Bretskyan hierarchy theory (Spiridonov & Eldredge, 2024)). The variety and abundance of these hierarchies in science is a manifest of both: hierarchical world structuring and the utility of the hierarchical approach to simplify, understand and explain its structural complexity. However, it is beyond the scope of this work to explore all the hierarchies established in science, let alone those used in biological sciences. Instead, common qualities of various hierarchy theories, along with their construction principles and limitations will be reviewed in this section.

Also, one hierarchy theory among all is selected as the foundation in this thesis; one that is believed to be most appropriate in explicating spatiotemporal biota organisation across many scales, with a great emphasis on abiotic drivers. This theory is Bretskyan hierarchy theory (Spiridonov & Eldredge, 2024). Why it is so, should become clear in the following sections, as the beneficiary features of the approach will be listed. This theory will be instrumental in interpreting the results obtained with methods developed within the framework of this thesis as well as evaluating their value. These methods and case studies along with the interpretations are presented, herein in the fourth chapter of the thesis. Also, other methods commonly used to study spatial and temporal biota organisation that are overviewed in the third chapter of the thesis will be as well evaluated and compared with the proposed methodological approach in terms of how well their principles and qualities align with the Bretskyan hierarchy framework. As such, this theory will be presented and elaborated to some extent in the following section of this thesis chapter. Though readers should refer to the original text by (Spiridonov & Eldredge, 2024) for the most comprehensive familiarisation.

Note that although the focus here is on Bretskyan hierarchy framework, other hierarchical approaches that share particular characteristics (specifically, spatial or temporal contiguity, nested compositional structure (e.g. patchy mosaic), explicit boundaries in space or time and the capacity to be established from empirical data) could benefit from the application of the developed and presented methods in this thesis. As the discussions about the nature and emergence of structural complexity in previous section (specifically see section The Apparent Order of Patches and Smoothness, and Entities as Patches) showed such hierarchical organisations (from hereafter referred to as "patch hierarchies") should be common in physical world.

1.2.1. Concept

A hierarchy is the organisation of entities into a layered structure of levels, based on one or more traits such as size, rate, functional importance, structural or compositional relationships, or level of control. Layering is the most prominent characteristic of hierarchical organisation and of complexity more broadly, as it is a common feature of many complex systems (Ahl & Allen, 1996; Salthe, 1985; Simon, 1962). Additional traits that define individuality—such as specific functions, system boundaries, and self-integrity—serve to distinguish discrete entities within each hierarchical level.

1.2.2.Control and Compositional Hierarchies

In the "Shrek" movie, when Shrek, the ogre, tried to explain complex causes of his behaviour that perplexed his loyal companion Donkey, he referred to an onion: "Ogres are like onions. […] Onions have layers. Ogres have layers! Onions have layers. You get it? We both have layers". Later in the movie Donkey goes on to suggest that Shrek could be a cake instead of an onion because they are also layered. Although the metaphor and its context may appear inappropriate for academic context, it offers a very simple and common to live representation of the two fundamental types of hierarchies according to which the material world is structured as suggested by Salthe (1985) (Figs. 1, 2). "Onion hierarchies" would represent compositional hierarchies wherein each entity is nested within other entity (e.g. cell inside human, human inside building, building inside Milky Way galaxy). "Cake hierarchies" would then represent control hierarchies wherein entities from higher levels exhibit more control over entities at lower layers (e.g. army command, trophic relationships). What these two metaphorical representations of hierarchies are missing are individuals – avatars that represent the entities (e.g. berries in a cake seen in Figure 1).

Figure 1. Compositional (left) and control (right) hierarchies as onions and cakes, respectively. Sources (licenced free for non-commercial distribution): Onion photo from https://pixabay.com/, cake photo by Anna Belousova from https://www.pexels.com/.

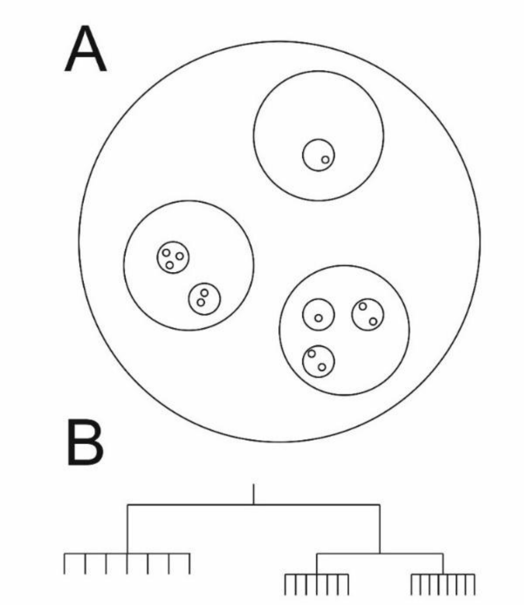


Figure 2. A – compositional hierarchy, B – Control hierarchy. Recreated modified after Salthe (1985).

Control hierarchies can be either nested or non-nested, since interactions between entities often transcend simple, one-way, top-down asymmetrical relationships as represented by hierarchical pyramids. This is so due to feedback loops, multiple entities on top and their downstream interactions (Corominas-Murtra et al., 2013). As such they are better represented as uni- or even bi-directional graphs. Compositional hierarchies are always nested by definition, but they may vary from strict nesting (i.e., entity can only be nested within single entity) to heterarchy (i.e. the same entity is nested within several entities). Both types of nesting are possible within the material world, depending on the perspective (e.g. reeds are nested both within water they are immersed, and within the air; or reeds are nested within lake ecosystem, which is nested within broader ecosystem). Heterarchies become widespread in diachronic (i.e. those that span time) real-world compositional hierarchies containing mobile entities (e.g. migrating birds are nested within ecosystems that can be on even separate continents, depending on a season). All physical entities, and more generally all material world, is organised according to both type of hierarchies: compositional and control (Salthe, 1985). As discussed in previous section, the world can be conceptualised as a dynamical hierarchy of nested patches that interact with (i.e., control) each other and energy gradients (Wu & Loucks, 1995). Thus, real-world hierarchies should include both organisational principles.

That material world is organised compositionally and control-wise also means that each physical entity can be viewed from either perspective. This leads to a varying emphasis on either aspect (compositional or control) in different hierarchy theories. For instance, ecological community hierarchy seems to give more emphasis on composition, whereas ecological ecosystem hierarchy – to the aspect of control since identities of particular species and organisms are not of interest in that hierarchy theory but their functions, associated processes, and their rates are; since different species and organisms can serve the same function in an ecosystem (Allen & Hoekstra, 2015; Allen & Starr, 1982, 2017; O'Neill, 1986). Bretskyan hierarchy theory is an intersection between control and composition hierarchies (Spiridonov & Eldredge, 2024).

1.2.3. Repetition, Surfaces, and Spatiotemporal Contiguity

Perhaps the most fundamental assumptions of hierarchy concept are that of existence of entities as distinct classes of observation and of their redundant and observable repetition (Ahl & Allen, 1996). These assumptions at the same time imply the complexity of world through the existence of number of different entities (essences or general patterns; note that this is a broader concept than that of physical entities which occupy space and must be somehow observable), and the simplicity of it through the redundant and observable repetition of these entities. Each repetition of an entity is a discrete individual (entity avatar); and for it to be observable it must have a recognisable surface or boundaries which allows to distinguish it from the background and other individuals (Ahl & Allen, 1996; Salthe, 1985). In real-world nested material hierarchies these individuals must have surfaces that are recognisable in both spatial and temporal dimensions (Ahl & Allen, 1996; Eldredge, 1985). These surfaces of individuals, more specifically their outer boundaries, must also be contiguous in both space and time due to the compositional nature of material world (i.e., each physical entity occupies space). Thus, real-world hierarchies should be composed of contiguous patches, representing physical entities. The fundamentality of all these assumptions lies in the fact that the abundant majority of scientific and philosophical approaches hold these assumptions as well. Bretskyan hierarchy theory also considers the existence of physical entities that have spatiotemporal contiguous boundaries.

1.2.4.Holons and Triadic Perspective in Hierarchies

Each level of entities can be approached as a separate dynamic system, though a more inclusive and effective approach is that of a triadic perspective recognising holons (Eldredge & Salthe, 1984; Salthe, 1985). Holons – the term dubbed by Koestler (1967) – are entities that at any level of a hierarchy simultaneously are parts and wholes, facing upward and downward hierarchical relationships (Eldredge & Salthe, 1984). Such triadic approach invites the distinction of two types of causes for explanation of phenomena – causes that come from the lower level (initiating conditions or constraints) and those that come from the upper level (boundary conditions). Boundary conditions are represented by stable constants, while limiting conditions – by dynamic averages of rapidly fluctuating values. These types of causes are non-trivially linked to Aristotelean classification of causes (Eldredge & Salthe, 1984; Salthe, 1985). The middle, focal level has observable dynamics represented by 'normal' variables, as well as its own causes due to the interaction of system components. Even though in some cases consideration of more than three levels are necessary (e.g. extinction of all individuals, populations, and demes also means extinction of species), triadic approach is elegant and effective due to its parsimony and the balance between reductionism and holism.

1.2.5.Principles Governing the Distinction and Ordering of Hierarchical Levels

Emergence is very important phenomenon to hierarchy theory. It occurs when something unexpected, spontaneous appears at the upper levels not foreseen from the dynamics of lower levels. Common emergence example is wetness quality of water – we cannot observe it at the level of singular water molecules. In a sense, emergence is a development of new boundary conditions that is somehow caused, but unexplained or the explanation is too complex considering only the dynamics of lower levels. Thus, emergence corresponds to changes in states of higher-level entities (e.g. birth-death). This means that the phenomenon of emergence is vital for the recognition and creation (Salthe, 1985) of higher levels entities, since it explains the rationale why the recognition of only lower-level entities is not enough.

Other authors underscore differences of rate of processes as the ultimate principle behind the appearance of different entity levels and their ordering: lower-level dynamics tend to be much rapid than the dynamics of higher-level entities (Ahl & Allen, 1996; O'Neill, 1986; Simon, 1962; Wu, 2011). This approach stems from the recognition that most hierarchical systems have a trait of near-decomposability and the notion of “empty world hypothesis” (Simon, 1962). In a nearly-decomposable system, composed of subsystems, interactions between subsystems are much less frequent than interactions within each subsystem. The “empty world hypothesis” is a generalisation of this trait suggesting that only a small fraction of all interactions is necessary in describing some system, and we can effectively ignore most, less important, weaker, less frequent, and more distant interactions; so, in a sense, a world is practically empty of meaningful interactions. This approach is quite similar in spirit to the triadic approach which ignores interactions in all but three adjacent levels of hierarchy since both approaches simplify the world by ignoring “less important” interactions.

Other criteria for serial ordering of hierarchical levels and their recognition in general include but are not limited to scaling of numbers, magnitude, connectivity, time, and space (Allen & Hoekstra, 2015; Wu, 2011). Some general principles for ordering of hierarchical levels in ecology as provided by Allen (2009) and summarised by Wu (2011) are:

1. Slower operation and lower frequency at higher levels.
2. More control is exerted from higher levels to lower levels.
3. Higher levels provide context for lower levels.
4. Integrity is lower and connections between holons are weaker in higher levels.

5. Entities of higher levels consist of entities of lower levels, if hierarchies are nested (remember that compositional material real-world hierarchies can all be considered nested (Eldredge, 1985; Eldredge & Salthe, 1984; Salthe, 1985))

Based on other literature (Allen & Hoekstra, 2015; Allen & Starr, 2017; Eldredge, 1985; O'Neill, 1986), we can also add that higher levels, especially in compositional material real-world hierarchies, should also exhibit 1) higher importance, 2) larger temporal and spatial extents, and 3) higher quantities of energy transferred / higher magnitudes of phenomena (e.g. hierarchy of ecological disturbances). Though, probably the most significant requirement in ordering hierarchical levels, as mentioned before, is the emergence, for entities from different levels must be significantly different from each other to effectively summarise a behaviour of a system, as opposed to being a mere aggregation of lower level entities (O'Neill, 1986). Also, to provide the most parsimonious but still accurate perspective towards the functioning of a system in question, the number of entity levels distinguished should be balanced (no more and no less than necessary). This is the main reason why hierarchy theories are truncated (e.g. there is no reason to go down to the elementary particles and up to the universe in biotic hierarchies, at least at the current level of knowledge) and why the number of levels distinguished in various hierarchy theories is usually small (e.g. no more than ten).

To conclude, the notion of hierarchy at its broadest sense involves the recognition of the existence of general patterns (entities) and their redundant repetition (individuals / entity avatars), as well as scaling or layering of these patterns according to some underlying logic (levels). The fact that hierarchy theory is used in distinguishing and defining important entities and their relationships makes it and its applications very fundamental, with a huge potential in creating and shaping new paradigms as well as reforming the old ones.

1.2.6. Progression of Knowledge Limits Across Hierarchy Levels

Several important practical consequences resulting from principles listed before that govern the distinction and ordering of levels in various hierarchy theories are noted. Most important in the context of this thesis, is that they mean that entities residing at higher hierarchical levels are harder to study and are likely to be less researched and understood, despite their typically higher importance.

First, the fact that level ordering is often based on size, duration, integration (which effects boundary fuzziness) and tempo of dynamics means that the more entities in these respects are further away from what humans can naturally perceive, the harder is their observation and the more sophisticated tools are involved in it. Thus, this hinders the understanding and research not only of large-scale entities, but also of very small-scale entities. The study of entities far removed from our scales is dependent on development of techniques and technologies permitting observation.

Second, the fact that entities at higher levels tend to exhibit slower dynamics means that per unit of time they tend to generate less data about their behaviour. This potentially decreases the range of behaviour that could be observed, especially if the entity's observable history is relatively short to the tempo of entity's dynamics. Essentially, this means that such entity's will produce fewer natural experiments that could be investigated in order to understand them. For example, only three supercontinent cycles occurred over the last 2 billion years (Mitchell et al., 2021). Also, less data translates into lower statistical significance of results, or even their unsuitability for the application of statistical analysis. This slow tempo may also inhibit relating cause and effect in large-scale systems since the wait-time of system's response to natural or anthropogenic interventions can take too long and produce complicating causal chains. For instance, anthropogenic climate warming hypothesis was dismissed at first for the lack of accumulated evidence (Weart, 2011). In contrast, the same quality enhances the study of entities residing at lower hierarchical tiers (e.g. microbial communities), as their faster dynamics will generate much more data on their behaviour that will be easier to link with interventions.

Third, slower dynamics also inhibits human ability to perform controlled experiments because of long waiting time of system's response to experimental intervention. Controlled experiments are also inhibited by the fact that large-scale systems typically involve more energy and higher magnitudes of phenomena. This means that much more effort may be required to impact their state. These experiments are not only less feasible but also limited by ethical considerations because high-tier, large-scale entities are usually more important and constitute boundary conditions for lower-tier entities (e.g. humans, local ecosystems), exerting stronger control over them. Conversely, faster dynamics, lower energy involved, lesser importance of low-tier entities should permit controlled experiments much more frequently.

Finally, in nested compositional hierarchies, higher-tier entities are much more complex (i.e. have many more components and subcomponents) than low-tier entities. As such the number of interactions that can occur within them and that may require consideration can be much greater in these entities due to properties of combinatorics.

Collectively, these implications should result smaller amount of accumulated knowledge about large-scale entities despite their higher importance, and much better understanding of microscopic, and especially macroscopic entities (entities residing at or below the scales of humans). While this is not another principle to be followed when distinguishing and ordering levels of hierarchies, it is still important consequence resulting from the application of other principles, determining the limits of knowledge across layers of hierarchies.

1.2.7. Limitations of Hierarchy Theory

Some critiques of hierarchy theory stem from misunderstandings about its nature and scope (Wu, 2011). It is often criticised for lacking a unified methodological framework, a common set of principles applicable across its various formulations, and a precise mathematical structure. However, if hierarchy theory is understood in the sense proposed by Allen (2009) —as a form of general theory intended to provide conceptual scaffolding rather than generate specific predictions—such criticisms appear to be misplaced (Wu, 2011). Moreover, several specific variants of hierarchy theory do, in fact, generate testable hypotheses and predictive frameworks (e.g. Spiridonov & Eldredge, 2024).

Another important limitation of hierarchy theory worth examining concerns the ontological status of the entities and hierarchies it posits. The reality of hierarchical structures has long been debated (Ahl & Allen, 1996; Allen & Hoekstra, 2015; Allen & Starr, 2017; Eldredge, 1985; Miller, 2008; Salthe, 1985; Simon, 1962; Wu, 2011). Some scholars argue that hierarchy theories are inherently provisional or even inevitably flawed, yet still useful as conceptual models constructed by subjective observers (Ahl & Allen, 1996; Allen & Starr, 2017). This perspective introduces a key distinction between so-called “empirical” or ontological hierarchies—those that exist independently of human perception, akin to Kantian noumena—and “definitional” hierarchies, which are observer-dependent constructs aimed at approximating these underlying structures (Ahl & Allen, 1996).

This distinction aligns with recent insights from neurobiology and psychology, which suggest that the human mind has a remarkable capacity to generate and reshape conceptual categories—processes that in turn influence perception in ways that reinforce the newly formed concepts. For instance, the introduction of colour concepts lead to the perception of discrete colour bands in a rainbow, despite the underlying mostly smooth spectral gradient.

Similarly, the development of new emotion concepts can give rise to the subjective experience of previously unrecognised emotional states (Barrett, 2017). In this regard, human cognition functions similarly to a classification tree model (Breiman et al., 1984), seeking and imposing thresholds within continuous variation to minimise predictive error—e.g., categorising observations based on decision rules such as "if x < threshold, then classify as y."

Because new concepts are often constructed through combinations of existing ones, they can yield even logically inconsistent or physically implausible ideas (e.g., "wet and cold dark fire") that may nonetheless shape perception and reasoning (Barrett, 2017). Given that there are numerous legitimate ways to define system and entity boundaries (Ahl & Allen, 1996), this reinforces the need for caution when interpreting hierarchical constructs. The distinction between ontological and definitional hierarchies serves as a critical reminder of the epistemological limitations inherent in all attempts to model complex systems.

However, this distinction between empirical and definitional hierarchies may offer little beyond the explicit and cautious acknowledgment that scientists, as human beings, are fallible and that any model of reality is inherently distinct from reality itself. Under this view, even the most robust and well-developed definitional hierarchies can never be confidently claimed to accurately represent unobservable empirical hierarchies. Consequently, the validity of a hierarchy is judged less by its ontological accuracy and more by the value—economic, epistemological, or societal—that can be derived from its practical application.

Advocates of this perspective tend to adopt a more process- and scale-oriented approach, focusing on differences in rates of processes rather than on the entities themselves. They often criticise traditional biotic hierarchies for conveying a potentially misleading impression of strict, scale-based nesting—such as the assumption that organisms are always smaller than communities and composed of smaller sub-entities (Allen & Hoekstra, 2015). Moreover, they highlight the fuzziness not only of entities above the level of organisms but sometimes even of the organisms themselves, citing examples such as aspen and banyan trees or the colonial Portuguese man-of-war (Allen & Hoekstra, 2015). While such "less-things, more-process" approaches have demonstrated their usefulness, they contrast with the argument that the explicit recognition of biotic entities and their relationships remains a foundational aspect of biology—one that has contributed significantly to the field's development (Wu, 2011).

Meanwhile, other hierarchy theorists explicitly accept various entities—such as species and organisms—as ontologically real individuals, and argue that the reality of hierarchies themselves is self-evident. In fact, the ontological reality of entities is regarded as a critical requirement in some hierarchy theories (Eldredge, 1985; Eldredge & Salthe, 1984; Miller, 2008; Salthe, 1985). These frameworks tend to adopt a strictly compositional and control-based view of hierarchy, in contrast to certain ecosystem-based hierarchies—such as hierarchical food webs—where the control aspect is more strongly emphasised (e.g. O'Neill, 1986). Nevertheless, even within this entity-oriented camp, concerns have been raised about the foundations of hierarchy construction. For instance, Eldredge (1985) cautioned that "we had better get our ontology straight and worry about such questions as the actual existence of demes in nature," underscoring the importance of ensuring that the hierarchical levels include real, biologically meaningful actors involved in evolutionary and ecological processes.

In this sense, ontological commitment can be seen as a potential vulnerability in thing-oriented hierarchies: the omission of a real entity or the inclusion of a spurious one may undermine the entire framework. However, rather than reinforcing a dichotomy between process-oriented and entity-oriented views, a more productive path lies in seeking common ground. On one hand, it is reasonable and often useful to treat some perceived beings—particularly biotic entities—and their hierarchies as ontologically real. On the other, we need not assume that our hierarchical theories must be ontologically perfect to generate valuable insights and practical outcomes. The fact that hierarchy theory can accommodate both perspectives—one grounded in ontological realism and the other in pragmatic constructivism—can be seen not as a weakness due to conceptual vagueness, but as a testament to its flexibility and generality.

Another general limitation of hierarchy theory lies in how it leverages the principle of near-decomposability (Simon, 1962). The emphasis here is on the prefix "near". While the natural world is indeed in many respects near-decomposable—exhibiting relatively stronger interactions within subsystems and weaker interactions between them—hierarchy theory often proceeds as if full decomposability were the case, framing the world as composed of clearly delineated, nested systems and subsystems. While omitting weaker interactions may serve as a useful heuristic to reduce complexity, it also risks introducing significant biases. As discussed earlier, this simplification can shape perception, rendering us empirically blind to interactions deemed negligible between more distantly related systems (Barrett, 2017). The crux of the problem is that the world consists of multiple, overlapping, and interacting systems, yet we are the ones defining their boundaries. These boundaries often mirror the institutional and conceptual divisions of scientific disciplines (Spiridonov & Eldredge, 2024). As a result, the ways in which science is structured—and the ways in which scientists are trained—bias our perception of nature toward systems that conveniently align with disciplinary domains. This tendency reinforces a worldview that privileges nested, internally coherent systems over those that transcend disciplinary or systemic boundaries. In light of this, it is perhaps unsurprising that different biological (sub)disciplines have developed their own hierarchy theories, as reviewed by (Spiridonov & Eldredge, 2024).

Do the boundaries between scientific fields correspond to the "weaker interactions" among the components of the systems they study? The very question may appear absurd, especially in cases where the same biological or physical objects are investigated across multiple scientific domains. For example, reef-building organisms are central not only to community ecology but also to ecosystem ecology, landscape ecology, evolutionary biology, sedimentary geology, and other disciplines. These overlaps illustrate that the problems addressed in different scientific fields are often non-trivially interconnected and emerge from a single underlying system that is artificially subdivided by disciplinary paradigms. These paradigms, in turn, define which scales, processes, and observables are considered most relevant.

Consequently, study objects that are shared across disciplines may be better viewed as hubs of scientific inquiry—nodes of strong, not weak, interaction—undermining the assumption that disciplinary separations align with the principle of near-decomposability that hierarchy theory often invokes. This observation suggests that hierarchy theories developed within distinct but interconnected (sub)disciplines are often narrower in scope and less capable of encompassing the full complexity of the systems they describe. Such theories may fail to account for important cross-scale processes, not because of inherent theoretical limitations, but because of how disciplinary boundaries shape their application. Thus, the critique here is aimed less at hierarchy theory itself and more at the way it is often applied—along artificial disciplinary divisions that obscure the true system boundaries.

An example of good theoretical practice is the 'dual hierarchy' model (Eldredge, 1985; Eldredge & Salthe, 1984), which integrates genealogical and ecological process hierarchies into a unified framework. This model recognises that organisms are simultaneously embedded in both ecological and genealogical hierarchies, and that their ontogeny—shaped by both contexts—has cascading effects on entities at both higher and lower hierarchical levels. From this example, and from the variety of biotic hierarchy theories discussed earlier, one might conclude that there is no single universal hierarchical structure governing the biotic world. Rather, there appears to be a multitude of competing process hierarchies, each shaping biota at distinct scales and along different dimensions. While this pluralistic approach may be closer to biological reality, its complexity often limits practical applicability. In striving to manage complexity by omitting ‘weak interactions,’ science may inadvertently generate a profusion of disconnected hierarchies and competing frameworks—leading to conceptual fragmentation rather than clarity. The dual hierarchy model itself has not escaped critique for this reason, having been described as overly complex and difficult to apply (Gould, 2002; Rosenberg, 2022).

In this light, the Bretskyan hierarchy theory represents a more integrative and tractable alternative. It could be seen as a conceptual “suture zone” linking biology, ecology, landscape ecology, evolutionary biology, macroecology, macroevolution, (palaeo)biogeography, geography, geology, and even plate tectonics, as well as geodynamics (Spiridonov & Eldredge, 2024). The theory explains discontinuities in matter, energy, and information transfer across temporal and spatial scales from a unified perspective grounded in real-world structures. While it implicitly acknowledges the influence of various biological and geological process hierarchies in shaping its entities, it does not rely on the explicit application of all those hierarchies to delineate Bretskyan units. Instead, it adopts a patch-based compositional and control hierarchy model, recognising spatiotemporally contiguous entities—such as holobionts and geobiomes—with clearly defined boundaries in both space and time. This grounding in discrete, observable phenomena gives Bretskyan hierarchy a high degree of ontological realism. Owing to its synthetic scope, real-world anchoring, and conceptual novelty, Bretskyan hierarchy theory is the primary theoretical framework adopted for interpreting the empirical results presented in this thesis.

1.3. Bretskyan Hierarchy Theory

As the Bretskyan hierarchy theory and its empirical applications form a central component of this thesis, this section presents an overview of the theory primarily as developed by Spiridonov and Eldredge (2024), with occasional interpretative additions and implications relevant for the design of a methodological framework or the interpretation of empirical case studies. To maintain textual flow, repeated in-text citations to Spiridonov and Eldredge (2024) are mostly omitted. Given that this publication currently represents the only work dedicated exclusively to Bretskyan hierarchy theory, nearly all uncited statements describing the theory in this section refer implicitly to that source—unless otherwise indicated as theoretical implications or authorial extensions. Readers seeking a more comprehensive account are encouraged to consult the original paper.

1.3.1. Concept

The Bretskyan hierarchy is a contemporary biological framework that synthesises genealogical, community, and ecosystem hierarchies—each representing a distinct dimension of biological organisation: information transfer, biotic interactions, and life–environment dynamics, respectively. Named in honour of American palaeontologist Peter Bretsky (first mentioned in the "Unfinished Synthesis", Eldredge, 1985), who first emphasised the discrete spatiotemporal distribution of biota, the Bretskyan hierarchy theory provides a model for understanding the nested, anastomosing structure of real-world eco-genealogical entities. These entities are typically polyphyletic, spatially bounded, compositionally stable, and functionally integrated assemblages of biological individuals that possess genealogical significance. That is, they can act as units of selection, possess reproductive capacity, have defined temporal bounds (with discrete origins and terminations), and exhibit genealogical continuity.

A defining feature of the Bretskyan hierarchy is its anastomosing—i.e. reticulated, braided river-like—structure: its units can undergo both splitting (fission) and merging (fusion) over time. The nestedness of the system reflects the compositional relationship among hierarchical levels: lower-tier Bretskyan units are constituent components of higher-tier units. The formation, survival, traits, and eventual dissolution of these entities are governed by interactions with the hierarchically structured physical world. In this framework, the hierarchical and nested organisation observed in the biosphere is ultimately imposed by analogous structuring in the abiotic world (Spiridonov & Eldredge, 2024).

Moreover, Bretskyan hierarchy theory incorporates the role of ecological interactions and ecosystem processes, which integrate biological individuals through coevolution and functional interdependence. Each Bretskyan entity is a spatiotemporally bounded, nested system comprising lower-level subsystems that participate in genealogical and ecological–economic processes. Accordingly, the Bretskyan hierarchy is a material compositional and control hierarchy: the control dimension is expressed through time-directional genealogical information transfer (e.g. ancestors determining traits of descendants) and through ecological feedbacks (e.g. abiotic dissipative systems control nutrient gradients which determine population sizes and distribution); the compositional dimension is represented by the strict nesting of smaller units within larger ones (e.g. intracontinental geobiomes nested within continental-scale geobiomes).

At the largest scale, the Bretskyan hierarchy converges with the Linnaean taxonomic hierarchy through the entity of Gaia—the global-scale geobiome encompassing all life on Earth (Spiridonov & Eldredge, 2024). Moreover, the theory interprets major transitions in individuality (e.g. eukaryogenesis) and key evolutionary events involving the expansion of life into novel environments (e.g. terrestrialisation) as the emergence—or birth—of fundamentally new Bretskyan entities (Spiridonov & Eldredge, 2024). Accordingly, the number and diversity of Bretskyan hierarchy units can be viewed as a proxy for the overall diversity of life from the perspective of geobiomes.

1.3.2. Geobiomes and Holobionts

In Bretskyan hierarchy theory, a fundamental distinction is drawn between holobionts (lower-tier units) and geobiomes (higher-tier units). At the lower levels, the hierarchy consists of holobionts—relatively small-scale individuals composed of multiple, mostly polyphyletic lineages, tightly integrated through functional interactions (e.g. a human and the diverse microbial communities residing within them). More generally, holobionts may be defined as “chemical reaction networks possessing functional and reproductive capacities”(Spiridonov & Eldredge, 2024). Holobiontic systems are dominated by biotic interactions, as most of the defining chemical reactions occur within and between the biological individuals that constitute the holobiont. Consequently, holobionts fall primarily within the domain of biological study.

It is important to highlight that holobiont spatial boundaries are typically formed by biological components specialised to isolate and regulate exchange with the external environment—such as cell membranes or epidermal layers. These boundary structures both filter environmental interactions and spatially bind internal components, effectively constraining and stabilising the system. The emergence of holobiont organisation is therefore a product of intense internal biological integration, reinforced and maintained by its biologically constructed boundaries. Each holobiont system possesses its own evolutionary trajectory (e.g. ontogeny), along with stable, system-specific pathways for the transfer of matter, energy, and genealogical information.

At larger spatial and temporal scales, the Bretskyan hierarchy encompasses more diffuse entities such as geobiomes—large, effectively isolated spatiotemporal systems of biota that are internally integrated through coevolution and ecological interactions, and externally bounded by geographical dispersal barriers (e.g. the African biota integrated with African abiotic systems). The discreteness—or individuality—of geobiomes, along with their genealogical and evolutionary significance, emerges as an effect of the prolonged, enforced cohabitation of biological lineages from polyphyletic taxa within a shared environment, isolated from other such groups. This sustained, spatially confined coexistence fosters intensive ecological integration and coevolution between constituent lineages and their abiotic environment.

The outcome of such integration is the emergence of a distinct biotic–abiotic system characterised by structured flows of matter, energy, and genealogical information, demarcated in both space and time. Each geobiome thus acquires a unique ecological identity, coevolutionary dynamics, and evolutionary trajectory—beginning when biotic and abiotic conditions stabilise into a coherent system, and ending when those conditions shift sufficiently to dissolve the system's internal integration. Bretskyan hierarchy theory explicitly links the formation and individuation of these geobiomic units to geodynamic processes, thereby underscoring the formative role of Earth's physical structure in shaping macroevolutionary patterns (Spiridonov & Eldredge, 2024). Given these attributes, geobiomes are primarily the domain of (palaeo)biogeography and historical biogeography, and thus constitute the central focus of this thesis. Accordingly, the following chapters will concentrate predominantly on geobiomes rather than holobionts.

Differences Between Holobionts and Geobiomes

As geobiomes occupy higher tiers within the Bretskyan hierarchy, holobionts are nested within them. Consequently, geobiomes are both spatially larger and temporally longer-lasting than the holobionts they encompass.

Unlike holobiontic systems—whose boundaries are defined by the physical and functional limits of specialised biological individuals—the boundaries of geobiomes are shaped by dispersal barriers. These barriers correspond to environmental conditions that restrict the movement and gene flow of biological components within the geobiome. While dispersal barriers can occasionally be biological in origin—arising from factors such as strong interspecific competition, pathogenic pressure, or parasitism—such cases are relatively rare. This rarity is due in part to the fact that limiting biotic conditions are often ultimately rooted in abiotic factors (Brown, 1995; Mayr, 1961). Moreover, biologically derived dispersal barriers typically affect only a small subset of species and are unlikely to define the boundaries of geobiomes at broader scales.

Therefore, it is primarily at the level of small, lower-tier geobiomes—such as those at the local or regional ecosystem scale—that biologically derived dispersal barriers are more likely to play a significant role. At higher hierarchical levels, geobiome boundaries are more typically shaped by broad-scale abiotic conditions, such as oceans, mountain ranges, or climatic gradients.

Because species have different environmental requirements and respond to different barriers, geobiome boundaries are inherently fuzzy and diffuse. Many biological individuals can survive—and often do persist—beyond the nominal boundaries of their geobiome. Furthermore, these boundaries can be ephemeral, as shifts in environmental conditions may alter the strength or position of dispersal barriers. The combined effects of this fuzziness and ephemerality can make geobiomes appear less ontologically real than holobionts.

This perception is further complicated by the fact that geobiomes operate at spatial and temporal scales far removed from those that humans typically experience. As such, they fall into the category of "hyperobjects" as described by Timothy Morton—entities so massively distributed in time and space that they elude direct human perception (Boulton, 2016). Similar examples of hyperobjects include climate change, evolution, plate tectonics, the solar system, galaxies, and even microscopic systems such as cells or bacteria. These entities often appear to us more as abstract concepts than tangible phenomena, because their detection and understanding require specialised analytical, technological, or computational tools—such as statistical methods, telescopes, or microscopes—and a degree of faith in the epistemic systems that produce them.

In contrast, many macroscopic holobionts exist at spatial and temporal scales comparable to human perception and often have clearly defined boundaries, which strictly enclose their components. Due to their high level of functional integration, any significant breach of a holobiont's boundary typically leads to systemic collapse or severe disruption, with escaped components generally unable to survive independently in the external environment. These characteristics make macroscopic holobionts appear more "real" to human observers than either microscopic holobionts or large-scale systems like geobiomes.

Another key difference between geobiomes and holobionts lies in the nature and frequency of interactions within each system. In geobiomes, interactions between the environment and holobionts occur far more frequently than interactions among holobionts themselves. This asymmetry stems from a fundamental difference: in holobionts, the matrix in which all interactions occur is biological, whereas in geobiomes, the matrix is primarily abiotic.

Moreover, in geobiomes, much of the transfer and cycling of energy and matter is facilitated by abiotic processes—such as solar radiation, river systems, ocean upwelling, volcanic ash fertilisation, and dust deposition—rather than by biological individuals alone, as is typically the case within holobiontic systems. As a result, life–environment interactions are central to geobiomic function and must be explicitly considered in any attempt to define or understand geobiomic systems.

This means that the identification and characterisation of geobiomes cannot rely solely on cataloguing the biological components of the system. It also requires detailed knowledge of the environmental processes that structure, sustain, and interact with those biological components. Consequently, the characterisation of the abiotic environment and its processes is an essential step in the definition and analysis of geobiomic systems.

Geobiomes and holobionts also differ fundamentally in their life–death dynamics and mechanisms of self-replication. Holobionts ensure genealogical continuity and the production of new individuals through sexual or asexual reproduction. This continuity of genetic material and biomass is transmitted upward to higher-level holobionts and to geobiomes, as geobiomes are composed of holobionts and are sustained by their ongoing biological processes. In this sense, holobionts help to "keep geobiomes alive."

However, in the case of holobionts, genetic similarity does not guarantee systemic similarity. The functioning and identity of a holobiontic system depend not only on its genetic composition but also on numerous traits that are not directly encoded by the genome. Many key characteristics—such as behavioural patterns, dietary preferences, the presence of parasites or pathogens, and the functional efficiency of component holobionts—are shaped by life history and interactions with the environment and with other holobionts.

This means that both the self-making and survival of holobionts are modulated not only by internal genetic programming but also by the higher-level Bretskyan systems—including both holobiontic and geobiomic units—within which they are embedded and whose processes they help to sustain. As a result, genetically distinct holobionts may converge functionally due to similar environmental exposures and systemic influences, while genetically near-identical holobionts may diverge significantly in traits depending on their specific life histories and interactions with higher-tier and lower-tier Bretskyan systems.

Thus, the development and persistence of holobionts are shaped by a combination of nature (gene flow) and nurture (matter and energy flow pathways). The dynamic interplay between these factors determines the process of holobiont self-making and links the fate of individual organisms to the broader hierarchies—both holobiontic and geobiomic—within which they are situated.

This leads to a concept analogous to group-level selection, as all holobionts—regardless of genetic relatedness—that assume identical roles within the same higher-order Bretskyan system during their life history have the potential to acquire similar, genealogically significant traits. Over time, higher-order holobiontic and geobiomic systems that foster or propagate pathological traits among their constituent holobionts are likely to either collapse or undergo transformation. Due to the high degree of integration within holobiontic systems, disruptions in just a few key components can trigger systemic pathogenesis (Dheilly, 2014). The death of a holobiont is absolute: when its internal integration is compromised beyond a certain threshold, the system collapses entirely, resulting in the death of all its components and preventing the re-establishment of a new holobiont system in its place.

In contrast, geobiomes are far less tightly integrated. Their survival does not hinge on the functionality of individual components to the same extent. During periods of intense systemic disruption, it is unlikely that all components will perish; those that survive can maintain genealogical continuity, allowing the system to persist. Consequently, disruptions must be far more substantial to threaten the integrity of a geobiome, and such disturbances are more likely to result in system transformation—that is, the emergence of a new geobiomic identity—rather than total collapse.

Moreover, because components of geobiomic systems are immersed in an abiotic matrix and interact predominantly with environmental processes, the stability of these abiotic processes largely determines the healthy functioning of the system, including the uninterrupted flow of genetic material and biomass production. Nevertheless, biotic interactions remain critical for system resilience. For instance, smaller, ecologically integrated geobiomic systems (e.g. at the local ecosystem level) may have fragile trophic networks, such that the extirpation of a single keystone species (e.g. a primary producer or a niche producing organism) could lead to systemic collapse.

More significantly, geobiomic systems can be “hijacked” by holobionts from other geobiomes expanding into their territory. This process introduces the concept of geobiome fitness and the idea of geobiome reproduction through expansion at the expense of other geobiomes (i.e. fusion or merger events). A geobiome’s fitness determines the outcomes of its interactions with other geobiomes and ultimately its long-term persistence. It is defined by the cumulative fitness of its constituent holobionts. Therefore, attributes of geobiomic systems that enhance the fitness of their resident holobiont taxa also enhance the geobiome’s overall fitness.

Paradoxically, long-term spatial and temporal environmental stability within a geobiome may promote narrow ecological specialisation and reduced taxonomic diversity. While this stability supports efficient and less disruptive survival and reproduction, it may render the geobiome more vulnerable to competition and incursion from neighbouring geobiomes. This vulnerability is comparable to the immunological fragility observed in organisms raised in sterile environments—while safe in the short term, such conditions produce weakened immune systems prone to failure when exposed to pathogens (Bloomfield et al., 2006; Zheng et al., 2020).

These parallels between geobiomes and holobionts, particularly in terms of systemic integrity, disruption, and evolutionary fitness, underscore the ontological reality of geobiomes as legitimate and functionally coherent entities.

The self-replication of geobiomes is enabled through the continued survival, reproduction, and geographical spread of their constituent taxa/populations/organisms or other biotic components, as well as the persistence of the abiotic systems that sustain them. When two geobiomes become spatially connected—such as through the formation of land bridges or seaways (e.g. the connection of South and North America during the Great American Biotic Interchange)—the process typically begins with the geographical expansion of abiotic environments that are capable of sustaining the biota of both systems. This expansion enables the dispersal of holobiont taxa into one another's geobiomic systems, often triggering disruption, reorganisation, and transformation in both.

This process is conceptually analogous to genetic recombination during sexual reproduction. Through the recombination of taxa assemblages, the identity of the geobiomes involved is altered. Following such a merger, a spatially larger and hierarchically higher “offspring” geobiome may emerge—

such as the Americas geobiome, formed from the integration of the previously distinct North and South American geobiomes.

These geobiome merger events are simultaneously emergence events: they not only transform the interacting lower-tier systems but also give rise to a new entity at a higher hierarchical level within the Bretskyan framework. The identity and structure of this emergent geobiome will tend to reflect more strongly the "parent" geobiome with the more resilient holobiont taxa, which are better able to withstand and adapt to the transformative pressures of the merger.

Nonetheless, the resulting geobiome will often retain spatially and compositionally recognisable lower-tier geobiomes corresponding to its parent systems. For example, within the Americas geobiome, a transformed yet still identifiable North American geobiome may persist, maintaining partial continuity with its pre-merger state.

Geobiomes can also reproduce through splitting, a process that occurs when a new dispersal barrier arises and separates the constituent holobiont populations of a geobiomic system—effectively fragmenting the system itself. A classic example is the breakup of Western Gondwana, which led to the eventual separation of South America and Africa. As spatial connectivity decreases, the overall integration of the parent geobiome declines, while the spatially separated subsystems may remain internally integrated. Over time, divergent evolutionary pathways—in both the biotic and abiotic realms—emerge within these isolated modules, eventually giving rise to new, hierarchically lower geobiomic entities, such as the African and South American geobiomes, which initially remain nested within the broader, still partially integrated Western Gondwana geobiome (see Example of Bretskyan Hierarchy section for a justification of why these units should remain nested within the same geobiome).

However, when integration within the original geobiome declines beyond a critical threshold—particularly if the newly formed geobiomes begin to integrate more closely with other geobiomes at their own hierarchical level (e.g. Africa with Eurasia, South America with North America)—the "parent" geobiome effectively dies, in the sense that it loses its individuality due to loss of systemic integration. This disintegration may be gradual, as the parent geobiome may persist for a time in a diminished state if the "offspring" geobiomes do not immediately integrate with new systems. In such cases, the collapse of the parent system may contribute to a broader decline in integration at its hierarchical tier—such as in the aftermath of the split of Pangaea, which resulted in reduced connectivity at the global geobiomic scale.

The collapse of the parent geobiomic system is of practical significance (see further elaborations in Triadic Approach to Bretskyan Hierarchy and Bretskyan vs. Bretskyan-like Hierarchy sections). Even long after such a split, the taxonomic composition of the resulting geobiomes may continue to show higher similarity with one another than with geobiomes elsewhere in the world, owing to their shared evolutionary history. This legacy persists even if the flows of genetic material, energy, and matter between them have been largely disentangled and replaced by new biotic and abiotic interactions. Thus, the collapse of a geobiomic system, when assessed through the lens of taxonomic similarity, may not be immediately evident. Instead, it becomes discernible only after a delay, likely correlated with the average lifespan of species (e.g. ~1 million years in mammals (Žliobaitė & Fortelius, 2022)), allowing for sufficient taxonomic divergence to accumulate between the separated systems.

Thus, the Bretskyan hierarchy exhibits two primary modes of reproduction that closely parallel cell fission and sexual reproduction in organisms. Reproduction via geobiome mergers resembles sexual reproduction and is typically more productive in terms of the number of potentially generated individuals and the creation of new hierarchical levels. For example, global mixing of marine biota is achieved over timescales of approximately 40 million years, providing significant buffering against abiotic perturbations (Spiridonov & Lovejoy, 2022). On the contrary, prolonged inability to merge can lead to range contractions in many genera and, eventually, to their extinction (as reported in brachiopods by Spiridonov et al. (2022)). These notions may appear paradoxical, as they seem to contradict the general expectation that diversity should increase under largely fragmented continental configurations due to elevated rates of allopatric speciation (Zaffos et al., 2017). Thus, the nature of diversity balance is not as straightforward as commonly assumed. In this light, the history of continental cycles—or more broadly, the history of dispersal barrier formation and dissolution—can still be understood as responsible for the reproductive history of the Bretskyan hierarchy, encompassing both the emergence and disappearance of its hierarchical tiers.

In addition, geobiomes exhibit a third, less common mode of reproduction: they can expand into biotically vacant environments through major evolutionary transitions in their constituent biotic entities. Examples include the colonisation of land by plants or the development of terrestrial ecosystems (terrestrialization). This is the only mode of reproduction that does not occur at the expense of existing geobiomes or via the creation of a new hierarchical level within an existing one. Instead, it involves the emergence of entirely new geobiomic systems in previously unoccupied domains.

Such reproductive events are associated with profound alterations to Earth's systems, including shifts in geochemical cycles, ocean chemistry, atmospheric composition, and sedimentation patterns. They also lead to increases in biological diversity and biomass production. Notably, this mode of geobiome reproduction most closely resembles holobiont reproduction in terms of the spatial separation and functional independence between the parent and the offspring geobiomes.

Taken together, these fundamental differences in structure, reproduction, and systemic dynamics between holobionts and geobiomes strongly support the conclusion that Bretskyan hierarchy theory constitutes a two-entity-class hierarchy—one that includes distinct but interdependent classes of biological organisation, each governed by its own rules of emergence, reproduction, and integration.

1.3.3. Triadic Approach to Bretskyan Hierarchy

According to the triadic approach outlined earlier, a comprehensive understanding and representation of a Bretskyan system requires the consideration of the traits and dynamics of three adjacent hierarchical tiers:

1. the supersystem (e.g. the continental geobiome) that encompasses the holon—the Bretskyan system of interest;
2. the system itself (e.g. the geobiome of a region separated from the rest of the continent by a mountain range); and
3. the subsystems that constitute the holon (e.g. smaller geobiomes further subdivided by major rivers flowing from the mountain range to the ocean or by other significant landscape features).

In addition, both downward and upward interactions—including the flow of matter, energy, and genealogical information—between adjacent hierarchical tiers must be considered. According to the triadic approach, it may seem that such information is sufficient to characterise the system’s boundary conditions and constraints, and to address fundamental questions: how the system operates, how it is sustained, what its vulnerabilities are, what conditions led to its formation, merging, or splitting, and ultimately, what may lead to its decline or extinction.

However, because geobiomes are fuzzy entities—akin to Timothy Morton’s concept of “hyperobjects” that are massive in scale, difficult to localise, and not fully graspable at once—it may be necessary to explore much deeper into the hierarchy. Specifically, we may need to extend the analysis down to the level of holobionts in order to fully understand the emergent macroscopic traits of geobiomes within and across the three adjacent hierarchical tiers and their complex interactions.

According to the triadic approach outlined earlier, to really understand and represent a Bretskyan system, one should consider the traits and dynamics of (1) supersystem (e.g. continent biota) that encompasses a holon - the Bretskyan system of interest, (2) system of the holon (e.g. biota of a region separated from the rest of the continent by a mountain range), 3) and subsystems that comprise the holon (biota of parts of the region separated from each other by major rivers flowing from the mountain range to the ocean or other major divides). Also, downward and upward interactions (matter, energy and genealogical information flow) between adjacent tier systems must be taken into account. According to the triadic approach this information should be enough to characterise system's boundary conditions, constraints, and understand the fundamentals such as how the system works, how it is sustained, what is its vulnerabilities, what conditions led to its formation, merging or split, and then to its ultimate demise. However, because geobiomes are fuzzy Timothy Morton's "hyperobjects", we may need to go all the way down the hierarchy to the tiers of holobionts to form an understanding of macroscopic traits of geobiomes within these three adjacent tiers of the hierarchy and their interactions.

In essence, no geobiomic system—nor its macroscopic traits—can be fully understood without reference to holobionts or other entities from adjacent biotic hierarchies (e.g. ecological, genealogical, or ecosystem hierarchies) that operate at comparable scales (such as organisms, communities, or species). Even if it were possible to characterise a geobiomic system solely in terms of the functions, macroscopic traits, and dynamics of its constituent lower-order geobiomes, this would still require prior knowledge of those lower-tier systems. Such knowledge, in turn, depends on information derived from better-known biological entities residing at the scale of holobionts or similar units.

This observation is supported by general principles of hierarchy theory, which state that our knowledge tends to be more advanced for lower-tier entities (see section Practical Implications of the Hierarchical Level Ordering Principles). Bretskyan hierarchy theory appears to conform to these principles as well (see section Traits of Bretskyan Hierarchy Units). This may help explain why nearly all frameworks—hierarchical or otherwise—that seek to describe living or socio-ecological systems include organisms at some level. Organisms occupy a central place in the taxonomic hierarchy, one of the most enduring and foundational hierarchies in biology. The taxonomic hierarchy organises organisms into nested categories (e.g. species, genus, family) based on traits that reflect phylogenetic relationships. These categories, particularly the species level, figure prominently in other biological hierarchy theories(e.g. Eldredge & Salthe, 1984; Gould, 2002; Miller, 2008; Salthe, 1985), as well as in diverse theoretical frameworks such as the sloshing-bucket theory (Eldredge, 2008), punctuated equilibria and coordinated stasis (Brett, 2012; Gould & Eldredge, 1993), and living systems theory (Miller, 1972).

Even frameworks that emphasise process and function—such as ecosystem hierarchy theory, ecological hierarchies, or the panarchy framework (Allen et al., 2014; Allen & Hoekstra, 2015; Allen & Starr, 2017; O'Neill, 1986) — ultimately rely on organisms and species. It is the species’ avatars that perform the functions and participate in the processes that these frameworks describe. Moreover, the traits of species ultimately determine the roles their avatars can assume in various ecological contexts. Although different species may fulfil similar roles in a given system, their specific traits define the range of conditions under which they can do so.

The prominent role of species and organisms in so many theoretical perspectives reflects the depth of accumulated knowledge about them. Their presence or absence, relative or absolute abundance, ecological roles, phylogenetic relationships, and other traits can yield valuable information about the systems in which they participate. This is especially important in the context of geobiomes. Taxonomic information, which inherently reflects phylogenetic relationships, can help identify disruptions in the flow of genetic material—that is, disruptions in the flow of genealogical information. Such disruptions imply concurrent disruptions in the flows of energy and matter and thus serve as indicators of geobiome boundaries. Additionally, an overview of the traits of taxa residing within a geobiome can inform us about their ecological functions and, by extension, the internal flows of energy and matter that sustain the geobiomic system.

Because geobiomes are defined by dominant life–environment interactions, abiotic conditions and processes must also be taken into account in order to further explicate the structure and functioning of geobiomic systems and to narrow down the ecological roles that individual species or populations play within them. In particular, geographical and environmental knowledge of potential dispersal barriers can provide valuable insights into the location of geobiome boundaries and the taxa they affect. In some cases, it may even be possible to delineate geobiomes based primarily on such abiotic features. A top-down approach to geobiome distinction could, in principle, be developed by sequentially identifying stronger to weaker dispersal barriers.

However, a purely abiotic approach faces several limitations:

1. Information on past dispersal barriers—especially in deep-time studies—is often scarce or highly uncertain.
2. The relevance of any given barrier is only meaningful when considered in relation to the dispersal abilities and ecological niches of the affected taxa.
3. Dispersal barriers may help define potential boundaries of geobiomes, but they offer limited insight into the internal dynamics and functional integration of the geobiomic system.

For these reasons, both biotic and abiotic information must be integrated to characterise geobiomes and to identify their macroscopic properties. When such information is available for geobiomes across three adjacent hierarchical tiers, the triadic approach (as discussed elsewhere in this thesis) can be applied to gain deeper insights into their structure, relationships, and dynamics.

To conclude, just as the theory of plate tectonics was ultimately recognised and explained through the synthesis of numerous well-understood, smaller-scale observations in the mid-20th century, our understanding of the emergent properties of geobiomic systems likewise depends on the integration of diverse strands of information—drawn from observations of smaller-scale entities and processes operating within these systems.

1.3.4. Example of Bretskyan hierarchy

To better illustrate the concept of the Bretskyan hierarchy, consider a real-world example from a terrestrial biota. The most significant dispersal barriers for terrestrial organisms are large bodies of water. Consequently, the highest level significantly integrated Bretskyan entities of terrestrial biota correspond to geographically isolated landmasses (all terrestrial biota of disconnected landmasses, or biota of two or more, more integrated landmass would also constitute Bretskyan entities of even higher levels, but they would be much less loosely integrated). The longer such landmasses remain isolated, the more endemic taxa they tend to accumulate, leading to increasingly divergent evolutionary histories and more and more distinct Bretskyan systems.

For instance, consider Mesozoic-Cenozoic India and Africa, as both experienced varying degrees of geographical isolation. During the early Mesozoic, these continents were connected as part of the supercontinent Pangea, a first-order Bretskyan hierarchical unit encompassing virtually all terrestrial life. When Pangea split latitudinally, two new second-order terrestrial Bretskyan units emerged: one corresponding to Laurasia and the other to Gondwana. India and Africa were part of the latter.

Around 110 Ma, Africa separated from South America (Rage & Gheerbrant, 2020), and India became fully isolated following its separation from Madagascar at approximately 84–92 Ma (Halliday et al., 2020). Each continent's biota thus formed a distinct Bretskyan system (i.e. a geobiome), embarking on separate evolutionary trajectories. Africa's biota became niche-unsaturated and depauperate, due to several extinction events unique to this "island Africa" (Fig. 3) (Rage & Gheerbrant, 2020). Whereas India accumulated endemic taxa and later established biotic connections with both Asia and Africa (Halliday et al., 2020).

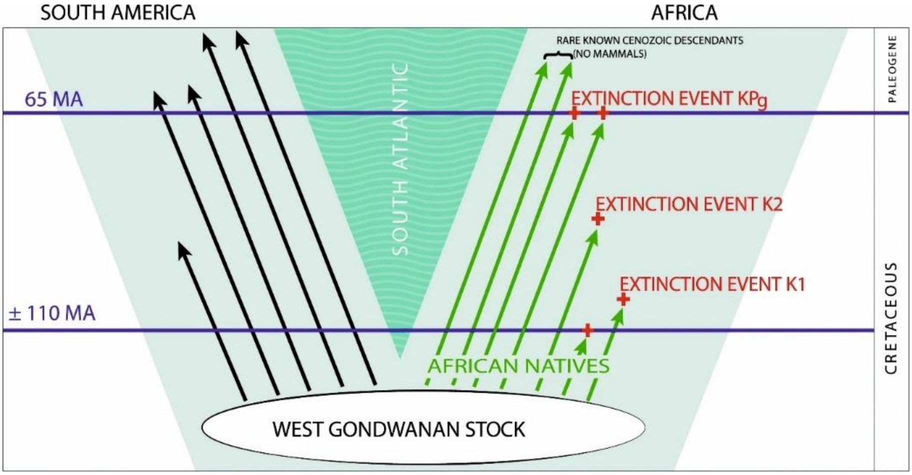


Figure 3. Diagram illustrating the macroevolutionary histories of South American and African faunas after their separation. Reproduced with permission from Rage and Gheerbrant (2020).

Eventually, India and Africa reconnected with Eurasia and became integrated into the Old World geobiome. The existence of these continent-scale Bretskyan units is supported by empirical evidence, such as palaeogeographical reconstructions and the clustering of fossil mammal taxa among Gondwanan continents when Gondwana was still intact but separate from Laurasia (Rage & Gheerbrant, 2020).

It is important to note that geobiomes of even long-disconnected continents—separated by vast oceans—can still engage in significant interactions. For example, once South America and Africa drifter apart and became separated by a newly formed Atlantic Ocean around 100 Ma BP, their geobiomic systems largely became disintegrated. However, there are evidence that rodents and monkeys of at least two separate primate lineages crossed the Atlantic Ocean on rafts as late as ~32 to 35 Ma (Sallam et al., 2009; Seiffert et al., 2020), colonising and populating South America. The possibility of such event is intriguing, emphasizing the discussed contingency in evolution of structural complexity even within mature biospheric system (see section Nested Complexity and Contingency on Low-Probability Conditions).

Importantly, interactions between these two continental geobiomes persist in the present day. The region now known as the Bodélé Depression in Chad since ~15 ka until ~1ka hosted an ancient Lake Mega-Chad with high diatom productivity (Armitage et al., 2015). Today, Saharan dust originating from this region ('magical dust')—enriched with minerals derived from those ancient diatoms—is thought to play a crucial role in sustaining the Amazon rainforest (Abubakar, 2017; Prospero et al., 1981; Swap et al., 1992; H. Yu et al., 2015). Phosphorus, a limiting nutrient in the Amazon, is delivered across the Atlantic Ocean during dust storms, providing essential support to the rainforest ecosystem and, by extension, to the organisms that depend on it. This example illustrates a vital, ongoing interaction between ancient African diatoms and contemporary South American biota, facilitated by abiotic processes that link the two continents.

In addition to such geochemical matter and energy transfers, biological connections also exist. Several migratory bird and marine species traverse the Atlantic, establishing regular biotic exchange between the continents. Examples include large-scale migrations by whales, sea turtles, fishes, sharks, birds (e.g. migrating arctic terns (Sterna paradisaeaand) (Luschi, 2013), Stercorarius maccormicki (south polar skua) (Kopp et al., 2011), among others (Bentley et al., 2025).

Such connections—whether abiotic or biotic—are important to consider, as they provide the basis for the existence of loosely integrated higher-level geobiomes that span across oceanic divides. For instance, interactions of this kind may support the conceptualisation of a New World + Old World geobiome, united not only by spatial proximity but also by functional and evolutionary linkages.

1.3.5. Dispersal Barriers

The concept of dispersal barriers holds central importance in Bretskyan hierarchy theory, as these features ultimately drive the individuation of geobiomes—one of the key foci of this thesis. Accordingly, they warrant detailed consideration. Spiridonov and Eldredge (2024) describe how the multifractal and scale-independent structure of the physical world results in a hierarchy of dispersal barriers, which in turn gives rise to an anastomosing hierarchy of geobiomes. They further note an analogy between dispersal barriers and sharp temporal transitions in biotic composition, suggesting that both represent abrupt environmental discontinuities—spatial and temporal, respectively. In this section, the role of dispersal barriers in structuring biota will be explored progressively, beginning with single-species ecological perspectives and expanding toward multispecies macroecological and macroevolutionary framework.

Definition

Typically, dispersal barriers are conceptualised as linear spatial features that delineate the limits of species or community ranges, often corresponding to prominent geographic landmarks such as mountain ranges, rivers, or marine basins. However, this conventional view is overly simplistic and warrants critical re-evaluation. Multiple aspects of this stereotype can be challenged, particularly when considering complex or cryptic environmental gradients, non-linear boundaries, or the influence of historical contingencies and ecological interactions in shaping species distributions.

To begin with a formal definition, dispersal barriers are spatially localised environmental conditions—such as unfavourable terrain, climatic extremes, or biotic interactions—that impede the movement of organisms (Caplat et al., 2016). Importantly, this definition implies that dispersal barriers are not inherently linear features; rather, they encompass the entire area across which such movement-restricting conditions are distributed. Consequently, spatial characterisation of a dispersal barrier may require consideration of two- or even three-dimensional spatial properties, including minimum and maximum width, length, shape, edge complexity, and as well as other geometric attributes.

Moreover, dispersal barriers do not always coincide with species range limits. They may restrict movement without strictly limiting the outermost boundary of a species' geographical range. Although the term "barrier" suggests complete obstruction, in reality, most dispersal barriers are semi-permeable. They often permit movement and temporary survival of individuals or even of small populations. Also, there is a continuum in how much permeable each dispersal barrier is. These considerations underscore the importance of barrier's properties that effect its permeability: size, shape, and internal environmental conditions determining its ecological function.

Another misconception inherent in the stereotypical understanding of dispersal barriers is the assumption that only prominent geographical features (e.g. mountains, water–land interfaces, escarpments) can create them. While it is true that such salient geographical landmarks often produce steep environmental and taxonomic gradients (ecotones), creating abrupt changes in conditions that constitute dispersal barriers for many species, numerous other, subtler factors can also establish effective dispersal barriers.

For instance, the absence of prominent geographical features, particularly in landscapes with low geological and topographical diversity, can itself act as a dispersal barrier. Species requiring diverse or abundant resources may find vast steppes, taigas, tundras, or oceanic zones uninhabitable due to limited resource availability and diversity. Prehistoric human settlement patterns in Lithuania illustrate this point, where settlements concentrated in topographically—and thus ecologically—more diverse landscapes (Daumantas et al., 2020). Consequently, species range limits may wind through expansive, seemingly mundane geographical areas lacking distinctive landmarks or obvious mobility-restricting characteristic.

Additionally, latitudinal climate zonation alone, independent of local or regional geological and topographical features, can create dispersal barriers and sink zones. Climatic factors such as humidity, precipitation, and temperature critically influence the survival and distribution of many species. Although mountain ranges often function as dispersal barriers due to rapid altitudinal climatic transitions (Whittaker, 1960), climate also varies spatially in the absence of significant altitudinal variation, influenced instead by latitudinal zonation and regional oceanic circulation patterns. These climatic conditions alone can generate dispersal barriers in unexpected, topographically or geologically uniform locations.

Moreover, continental size and configuration can significantly distort ideal latitudinal climate zones, potentially altering the orientation of dispersal barriers from latitudinal to longitudinal directions or shifting them from their anticipated locations. Similarly, ecological dispersal barriers can arise solely from interactions with incompatible species (e.g. strong competitors, predators, pathogens). If the ranges of these incompatible species correlate with prominent geographical features, the dispersal barrier may be considered as ultimately caused by geology or topography (Brown, 1995; Mayr, 1961). However, if their distributions align instead with latitudinal climate zonation, specific resource distributions, or overall resource diversity, the origin and nature of the dispersal barrier may be obscure.

Collectively, these subtle factors can complicate interpretations and obscure understanding regarding what ultimately constrains the geographical ranges of species or groups thereof. This emphasises the point that dispersal barriers inferred from fossil records or contemporary observations cannot always be explained by straightforward geological or topographical landmarks. Given our typically limited knowledge about past regional and local environmental conditions, we should anticipate encountering dispersal barriers—and thus species range limits—in unexpected geographical contexts.

Barriers as Population Sink Zones

Referring back to the discussions in Structural Complexity in Nature section, dispersal barriers may be understood as physical entities—such as mountain ranges or oceans—whose presence modifies nutritional, thermal, moisture, redox, or other energy gradients in ways that either divert organisms away from these zones or disrupt their dissipative systems. Alternatively, dispersal barriers can be conceptualised not as physical entities, but rather as zones in which multiple energy gradients become unfavourable for biotic entities, thereby redirecting them by various means. A more nuanced, interesting, and informative—albeit not entirely correct—perspective is to conceptualise dispersal barriers as potential population sink zones–areas characterised by negative population balances resulting from elevated mortality or reduced reproductive success. Such zones hinder movement not solely through physical obstruction, but through demographic attrition.

This view enables a binary classification of entire geographic space into potential sink zones (i.e. dispersal barriers) and potential source zones (i.e. habitats with a positive population balance). The term potential is used deliberately, following the distinction between realised and fundamental niches (Hutchinson, 1957): some environmentally suitable areas (potential source zones) may remain unoccupied because dispersal barriers prevent access. Inhabited source zones are potential source zones that were realized. The same logic applies to sink zones—those that are uninhabited are potential sink zones, while those that are inhabited despite being demographically unfavourable are potential sink zones that were realized. Semi-permeable, inhabited dispersal barriers thus correspond to realised potential population sink zones.

Barriers that are conventionally thought to restrict movement via physical obstruction (e.g. water–land interfaces, cliffs, escarpments) can also be regarded as potential sink zones, since entering such environments may lead to injury or death and are therefore actively avoided by motile organisms. However, this conceptual framework does not directly apply to organisms with passive dispersal modes—such as plants or plankton—whose movement is externally mediated (e.g. by wind, currents, pollinators, or herbivores). For these organisms, dispersal barriers may arise even within population source zones if imposed directional constraints restrict or prevent movement altogether. In some cases, the movement of even motile organisms can be modulated externally in a similar way within their source zones (e.g. by strong wind or currents). Thus, as initially stated this conceptualization of barriers as sink zones is not entirely correct as there are some dispersal barriers that are not potential population sink zones. Nevertheless, this framework could be useful.

Within this framework of barriers as potential population sink zones, the ecological attractiveness of a sink zone becomes a critical consideration. Some dispersal barriers may be naturally avoided (e.g., terrestrial species avoiding open water), while others may be entered occasionally due to neutral or ambiguous environmental cues. In some cases, highly attractive but ultimately inhospitable zones may act as natural ecological traps, offering short-term benefits while leading to long-term population decline (e.g. hazard-prone areas). Furthermore, environmental features such as valleys, canyons, or hydrological and meteorological processes (e.g., prevailing winds, river currents, or oceanic gyres) can act as funnels, directing organisms into sink zones. Thus, many dispersal barriers may be traversed or penetrated under certain conditions—particularly if their hostility is low, their ecological allure is high, their spatial dimensions are small, or if environmental funnelling concentrates movement paths through them. This suggests that large portion of species' ranges may consist of dispersal barriers.

Typical Patterns of Species Distribution

The explored characteristics of dispersal barriers, and the conceptual framing of these barriers as population sink zones, allow us to better understand and explain the irregular and intermittent nature of species distributions. As demonstrated by Brown (1995), species geographical ranges often exhibit numerous "holes"—areas devoid of occurrences—as well as "cool spots," areas of sparse occurrences, and "hot spots," areas of high occurrence density. Although "hot spots" typically cluster near the centre of a species' range, while "cool spots" and "holes" are more common at the range periphery, these zones can be arranged in varied configurations, enabling both sharply defined and gradually changing occurrence density patterns (Brown, 1995).

It is highly plausible that "hot spots" correspond to population source zones, whereas "cool spots" and "holes" represent dispersal barriers or sink zones. Given this interpretation, the existence of multiple population source zones interconnected by "cool spots" highlights the critical role played by the permeability of "hospitable" dispersal barriers in shaping the intricate, patchy distribution of species' populations and even in expanding their geographical range limits.

Soft (permeable to a large extent) dispersal barriers could be recognised from instances where occurrence density declines gradually in space, whereas hard (impermeable) barriers should correspond to zones marked by abrupt drops in occurrence density. Nonetheless, the many characteristics of these barriers—including their origin, size, shape, number, and the specific factors that limit or enhance permeability (such as environmental funnelling effects, ecological attractiveness, or moderate environmental harshness)—cannot be inferred solely from variations in occurrence density. To understand these aspects comprehensively, additional ecological, environmental, and organism-specific information is required.

Macroevolutionary Role of Dispersal Barriers:

Considerations above clearly indicate that the capacity of dispersal barriers to limit a species' geographical range is significantly modulated by their relative position within the network of the species' occurrence distribution. Hard dispersal barriers positioned near the centre of the distribution network have a greater potential to fragment the distribution, but a reduced capacity to limit overall range expansion, due to connectivity provided by surrounding soft barriers linking "hot spots". In contrast, hard barriers situated at the outskirts of the distribution network have less potential to fragment the occurrence network but possess an increased capacity to constrain geographical range.

Interestingly, it follows from this that hard dispersal barriers corresponding to spatial gaps in occurrences, or zones of rapidly declining population density, may drive allopatric speciation when located centrally within the distribution network as they fragment the population, yet allow dispersal outside the range, thereby contributing to the successful diversification of a lineage. Conversely, at the periphery of the distribution, hard dispersal barriers assume the opposite macroevolutionary role by preventing dispersal beyond the existing geographical range without fragmenting it.

These typically observed, relatively extensive species ranges (compared to the few, relatively small occurrence 'hot spots' or source zones), dominated by population sink zones (also known as dispersal barriers), as presented by Brown (1995), may not be random distribution features. Instead, they could represent macroevolutionary selected traits at, useful at species and even clade levels. Such fragmented yet extensive geographic ranges are beneficial at the species level because species with continuous, non-fragmented populations are more vulnerable to threats such as transmissible diseases, predation, or environmental changes, which can lead to extinction. Consider the example of the passenger pigeon (Ectopistes migratorius), which maintained an enormous yet spatially contiguous population and ultimately went extinct due to habitat loss and extensive hunting (Hung et al., 2014). Living exclusively within a single 'hot spot' is inherently risky, as worsening conditions in this location (transitioning from source to sink) can doom the species, especially if adjacent areas are also sink zones or dispersal barriers (i.e. constitute a sort of ecological trap). Additionally, species forming single, large populations are particularly susceptible to pathogens; a single, deadly outbreak could eliminate the entire species. Therefore, what might appear as ecological inefficiency—widespread yet fragmented occupation of marginal habitats—could actually represent an evolved safeguard, favouring species persistence by reducing existential risks associated with demographic unity. In this light, dispersal barriers that separate populations can be viewed not merely as an external environmental feature or a population sink zone but as an advantageous emergent, macroscopic feature of a species' niche.

Variations in species specialisation and niche breadth, leading to fragmented yet extensive geographical ranges dominated by population sink zones surrounding a few relatively small 'hot spots' (source zones), may also influence lineage-level traits such as species richness—traits that may be subject to clade-level selection over geological timescales. Such fragmented and expansive ranges (expansive relative to the size of source zones) are likely to increase the probability of allopatric speciation, thereby promoting lineage diversification and, in turn, enhancing long-term persistence.

Geographic isolation—and the para- and peripatric patterns it can take—inevitably more frequently occur in ranges fragmented by many dispersal barriers. Since the modern synthesis these isolation processes have been recognized as the principal engine of species-level diversification (Dobzhansky, 1940; Mayr, 1940) and continues to be emphasized in contemporary treatments (Eldredge & Gould, 1972; Rabosky, 2016; Spiridonov & Eldredge, 2024). As such we may expect more diverse clades to develop in lineages that historically contained species with niches whose geographical projections resulted in more fragmented ranges with many dispersal barriers.

Crucially, lineages with greater species diversity are expected to exhibit higher resilience to extinction. Biotic threats—such as pathogens, parasites, or the loss of symbionts—typically display a high degree of specificity towards particular species. This is important because species-depauperate clades may be disproportionately affected. For example, assuming minimal niche and range overlap among constituent species, if a pathogen eliminates a single species within a clade composed of only a few broadly distributed taxa, the resulting contraction in overall range would be significantly more severe than in a clade consisting of numerous, more specialised taxa occupying the same cumulative range. Notably, genus-level range size appears to be a primary determinant of extinction risk in marine animals (Harnik et al., 2012). Thus, biotically-driven species extinctions have larger impact on survival of species-poor clades via their range reduction. Furthermore, pathogen selectivity is non-random and tends to target phylogenetically closely related taxa (Gilbert & Parker, 2016), increasing the likelihood of entire clade-level infestations, exacerbating the mentioned risks when clades are species-poor.

Jablonski (1986) similarly found that during background (non-mass) extinction intervals, species-rich marine gastropod and bivalve clades exhibited longer survival times. He also reported that during mass extinctions, the survival of clades was not related to the range sizes of individual species but rather to the overall range of the clade (Jablonski, 2008). Because of ecological displacement, species-rich clades occupying a given total range must, on average, have constituent taxa with smaller individual ranges than those of species-poor clades. This is significant, as it implies that species-rich clades are not inherently more vulnerable during mass extinction events despite the smaller ranges of their component species.

Therefore, while fragmented and extensive geographical ranges may arise as species-level traits that reduce vulnerability through avoidance of demographic unity, they can ultimately influence lineage-level macroevolutionary trajectories by facilitating allopatric speciation and increasing species richness, thereby enhancing the long-term persistence of clades.

These ideas concerning the macroevolutionary role of fragmented and expansive species distributions, as well as barriers that fragment the ranges, at both the species and lineage (clade) levels are, of course, speculative. Nonetheless, they constitute empirically testable hypothesis and could be evaluated through comparative analyses of extant and extinct clades, using data on species distributions, diversification rates, and extinction, speciation histories.

Barrier Dynamics Over Time and Mass Extinctions

Environmental changes, which may shift and transform the structure of distribution networks and dispersal barriers over time, complicate the matters discussed. This complexity is amplified by the fact that such changes often occur differentially across space (Daumantas et al., 2022; Gedminienė et al., 2025). Environmental shifts can alter the relative positions of hard and soft dispersal barriers in relation to the distribution network, thereby impacting their roles in shaping species distributions and macroevolutionary processes.

Given that environmental change can also contract and ultimately dismantle the distribution network—potentially leading to species extinction—it follows that every inhabited location within a distribution network will inevitably function as a dispersal barrier or a range limit at some point in time. Thus, the question is not whether a particular location or geographical feature served as a barrier or range limit, but when it did so and, more critically, for how long relative to the lifespan of the species.

An insight that follows from this is that the strength of a dispersal barrier is best conceptualised not only as "harshness" of conditions or a degree of movement restriction but also as the magnitude of environmental change—or the duration of time—required for the conditions in that area to become suitable for habitation or at least to increase barrier permeability. All these three things (movement restriction, extremality of conditions and temporal span) are positively correlated in dispersal barriers (Spiridonov & Eldredge, 2024), but exceptions are possible. For example, water-land interfaces for many species act as almost impermeable dispersal barrier due to drastic change in environment and possible mobility modes. However, in some settings (e.g. very shallow shelf or lagoon next to a lowland) relatively little geological time and environmental change (e.g. minor sea level changes) may be required to shift these interfaces considerable distances, turning locations that were once hard dispersal barriers into population source areas. Dispersal barriers revealed from fossil occurrence data will more likely align with this temporal significance definition due to time averaged nature of the data.

This temporal perspective on distribution dynamics also allows for a meaningful connection between the concepts of extinction and dispersal barriers: extinction can be viewed as the consequence of the sustained and global expansion of dispersal barriers (i.e. population sink zones) across all population source zones. However, a complicating factor in this framework is that environmental changes driving the spread of dispersal barriers may also generate new potential source zones or open previously inaccessible ones via the creation of permeable dispersal corridors. Therefore, for extinction to occur, environmental changes must be of a nature that neither facilitates the emergence of new, accessible habitable zones nor improves access to existing but previously unreachable potential source zones. The idea is aligned with sloshing-bucket hypothesis (Eldredge, 2003, 2008) as less severe perturbations are likely to create or preserve accessible habitable zones, whereas more drastic changes may not.

Now imagine how all these matters discussed apply to collectives of populations across multiple species over macroevolutionary timescales. The range limits and dispersal barriers of different species will often not coincide, given their varied environmental preferences and tolerances. This discrepancy is especially pronounced in areas where only a few environmental parameters change. Such changes may act as dispersal barriers for a subset of species but remain irrelevant for the majority. Even in cases where dispersal barriers overlap spatially for multiple species, their strength and ecological impact may differ due to slight variations in tolerance thresholds among species with overlapping niches.

As a result, many dispersal barriers are expected to be selective, applying only to a limited set of species—or even to individual species. However, more formidable dispersal barriers—those that were more temporally and spatially stable and corresponded to abrupt and extreme changes in at least one critical environmental factor (e.g. temperature, oxygen levels, or salinity), or simultaneous shifts in multiple environmental parameters—are likely to affect a wide array of species over extended periods. This leads to a generalisation underpinning Bretskyan hierarchy theory: the stronger the dispersal barrier, the more species will succumb to it, leading to spatially isolated collectives of species that eventually integrate via coevolution and ecologic interactions. If such barriers—those affecting collectives of species—proliferate under drastically changing conditions, the likely outcome is the disintegration and fragmentation of larger, stable geobiomes into smaller, less stable units. These units become less stable and more transient because, during periods of perturbation, spatially and temporally shifting energy gradients that drive biodiversity are expected to continually shift dispersal barriers, thereby altering both the distribution of surviving species and the composition of local communities. Once conditions stabilise, and relatively constant energy gradients driving the distributions of collectives are re-established, larger and more stable geobiomes, along with longer-lasting locations of dispersal barriers, are expected to form.

Such predictions regarding geobiome dynamics during biotic perturbations are consistent with observed diachronic intercontinental (Cramer et al., 2010) and interregional (Alroy, 1998) patterns in the distribution of first appearances of new species (Radzevičius et al., 2016). These predictions suggest that the turbulence of biodiversity-driving energy gradients and the resulting dynamic patterns of dispersal barriers are primarily responsible for the observed diachrony in species compositions, rather than the notion that it simply takes time for species to disperse geographically once established. They also predict an elevated probability of extirpations (more likely) and extinctions (less likely) for both older (more likely) and newly emerged (less likely) species during periods of environmental perturbation. Furthermore, these predictions align with the heuristic macroevolutionary and palaeogeographic model of

(Radzevičius et al., 2016), which proposes that beta diversity should increase and alpha diversity decline during perturbations that drive abrupt and drastic species turnovers, while global diversity remains relatively stable due to speciation balancing extinctions. Finally, these predictions are empirically supported by study case of this thesis (see section: Discussion in Duration and structure of *Mulde/lundgreni* event).

These become less stable and transient because shifting conditions alter the distribution and composition of the surviving species. Once conditions stabilise, and the more or less constant energy gradients driving the distributions of collectives are re-established, larger and more stable geobiomes, along with the formation of longer-lasting dispersal barriers, are expected to form. Such predictions about geobiome dynamics are in-line with observed diachronic intercontinental (Cramer et al., 2010) and interregional (Alroy, 1998) distribution of first appearances of new species (not only it takes time for them to spread once conditions allow are favourable but also during perturbations their dispersal barriers are likely to be more spatially restricting and dynamic, leading not only to diachrony but also higher likelihood of extirpations), as well as heuristic macroevolution and palaeogeographic model of (Radzevičius et al., 2016) that expects that beta diversity should increase, alpha diversity decline during perturbations driving abrupt and drastic species turnovers, while global diversity should remain more or less stable due to speciation balancing extinctions.

Building on the earlier proposition that extinctions result from the global spread of dispersal barriers, mass extinctions can be viewed as events driven by the worldwide expansion of particularly formidable barriers—those capable of bulldozing the entire geographical ranges of numerous species. Viewed in this way, mass extinctions may be seen as “too much of a good thing”: the very dispersal barriers that normally promote diversification and biotic differentiation, when globally pervasive and excessively severe, shift the macroevolutionary balance such that extinction rates surpass those of speciation. The global dominance of such formidable barriers during mass extinctions may also give rise to so-called ‘disaster taxa’—species capable of surviving in extreme, often unstable environments of widespread dispersal barriers. Following mass extinctions, as these barriers retract to moderate extents, speciation rates are expected surge as is often observed in the fossil record (Benson et al., 2016; Benton, 1995; Erwin, 2001). In this sense, the global spread and retreat of formidable dispersal barriers serve as temporal inflection points in the history of life, generating novel Bretskyan systems and effectively segmenting the Bretskyan hierarchy in time through large-scale biotic turnover.

Practical and Methodological Implications

A final, practically important point is that in most empirical cases, it is neither feasible nor realistic (due to various sampling and preservation biases) to investigate the spatiotemporal structuring of entire (palaeo)biotas. Consequently, most studies often focus on selected subsets of species, defined by taxonomic affiliation, dispersal ability, phylogenetic relatedness, ecological function, dietary preferences, or other traits. Crucially, this means that the geobiomes revealed in such analyses will differ from those that would be observed if the entire biota were considered. Relatively weak dispersal barriers (when viewed in the context of the whole biota)—for example, those associated with changes in soil type or the abundance of particular resources—may nevertheless produce sharp distributional boundaries within the subset of species under study. As a result, a greater number of dispersal barriers will be relevant, often leading to an inflated number and increased fuzziness of identified, group-specific geobiomes.

This also implies that boundaries between Bretskyan entities may sometimes be found in unexpected locations—mirroring patterns that were discussed in cases of singular species. The likelihood of such outcomes increases as the taxonomic scope narrows and the ecological or biological similarity among studied species increases. Therefore, phenomena often considered idiosyncrasies of ecology and evolutionary biology also carry significant implications for macroecology, macroevolution, and the practical applications of Bretskyan hierarchy theory.

To conclude, by progressing from ecological to macroecological and ultimately to macroevolutionary scales, we have observed how the role of environmental changes—and the dispersal barriers they generate—shifts in significance and function across hierarchical levels, giving rise to Bretskyan hierarchy systems. The importance of dispersal barriers is thus hard to overstate.

1.3.6. Traits of Bretskyan Hierarchy Units

Bretskyan systems can be characterised by:

1) Constraints: internal dynamics of matter, energy and heritable information transfer (e.g. the flow of genetic material as reflected in genealogic relationships between system components (holobionts and geobiomes) and corresponding genealogic trees, also ecologic interactions between system components (e.g. trophic networks, competition, coevolution,

invasion, migration), and interactions between system components and abiotic environment (e.g. pedogenesis, niche-building, natural selection)).

2) Boundary conditions: internal dynamics of matter, energy and heritable information transfer of parent system (examples are the same as above but figures interactions between parent system components)

The focus on these first two traits would constitute a triadic approach. The following traits would be a move beyond that.

3) External dynamics of matter, energy and heritable information transfer (examples are the same as above but figures interactions between system components and the components of other, less related Bretskyan systems of any hierarchical tier). Considering all of the external dynamics is not feasible and practical (as this leads to an overly complex view of the world that everything is connected to everything, thus nullifying the utility of a simplified and comprehensive perspective offered by hierarchy theory). Thus, only more important external dynamics should be considered (e.g. contemporary interactions between Africa and South America as provided in Example of Bretskyan hierarchy section).

4) Spatial and temporal properties (size, duration, shape)

5) Fitness level: likelihood of extinction (disintegration), longevity, resilience to changes, and ability to reproduce (cause changes in traits of other Bretskyan units, proliferate their traits and taxa to other Bretskyan units).

6) Hierarchical information (e.g. rank, hierarchic relationships with other units of the hierarchy, list of all components included in the system and all supersystems that encompass the system).

7) Level of integration (e.g. depth of coevolution, frequency and importance of ecological interactions).

8) Dispersal barriers that bound the system in space and time and their traits (number, origin, permeability, selectivity, size, duration, shape, and mechanisms they affect dispersal)

The following two traits are similar to the first 3, but differs in that they represent more disconnected and fragmental information, not causally tied together into comprehensive system of matter, energy and genealogical material flow. Nevertheless, they represent vital pieces of information in building the understanding of systems.

9) Miscellaneous information about system’s abiotic environment (e.g. palaeobiogeography, climatic conditions, ocean circulation, geochemical cycles).

10) Miscellaneous information about systems' biota (e.g. taxonomy, morphological traits, species-level traits).

Thus, systems structured according to Bretskyan hierarchy possess a wide range of essential traits that characterise their organisation and function. Importantly, Bretskyan hierarchy theory provides numerous predictions regarding how these traits should vary with a unit's hierarchical level and how specific traits interrelate (Spiridonov & Eldredge, 2024).

For instance, geobiomes situated at higher hierarchical levels are generally larger in spatial extent, longer-lived, and exhibit greater overall fitness. They tend to be defined by more formidable dispersal barriers, show weaker internal integration, and involve a larger number of internal and external interactions due to their greater component complexity. As a result, such systems are typically more complex but exhibit slower and more stable dynamics—characterised by fewer and less frequent shifts in the main pathways of matter, energy, and genealogical information flow that define the system.

In addition, the holobiont taxa encompassed by higher-tier geobiomes tend to be more taxonomically diverse, produce a greater number of progenies with more varied traits, and exhibit higher individual fitness. This, in turn, contributes to the increased overall fitness and resilience of the geobiome as a whole.

The fitness of a Bretskyan unit determines the resilience of its constituent lineages to environmental and biotic perturbations, as well as their reproductive potential. Consequently, when two Bretskyan units of the same hierarchical rank merge, the resulting unit is expected to more closely resemble the one with higher fitness. Typically, the more fit unit is the one that is larger and has persisted for a longer duration, as greater spatial and temporal scope correlates with exposure to a broader range of environmental conditions.

Taxa inhabiting areas characterised by higher environmental variability are expected to be more "learned"—that is, their genetic material encodes greater Fisher information about the environment (Spiridonov & Eldredge, 2024). As a result, taxa originating from larger and longer-lasting Bretskyan units may exhibit higher fitness, which is reflected in their increased survival potential, greater invasive capacity, broader geographic ranges, tolerance of a wider spectrum of biotic and abiotic conditions, and possession of more generalist traits.

When given the opportunity to invade the territory of smaller or younger Bretskyan units, such taxa are more likely to displace or outcompete native taxa. Thus, the fitness of a Bretskyan unit is directly related to the fitness of its constituent holobiont taxa, and it provides a basis for predicting the likely outcomes of interactions between geobiomes.

The manner in which various traits of Bretskyan entities—such as size, duration, pace of dynamics, and level of integration—change across hierarchical levels aligns well with established principles of level ordering in hierarchy theory (see section Principles Governing the Distinction and Ordering of Hierarchical Levels). This alignment suggests that general principles applicable to many hierarchical systems—such as the declining availability of knowledge about entities as their hierarchical level increases (see section Practical Implications of the Hierarchical Level Ordering Principles)—also hold within the Bretskyan framework.

Furthermore, the interconnections among the ten identified traits allow for predictive inferences: knowledge of a subset of traits can enable reasonably accurate predictions about others. This capacity makes Bretskyan hierarchy theory a powerful analytical tool for the study of biogeography, macroecology, and macroevolution. In particular, the ability to derive certain traits—such as hierarchical information (Trait 6) and temporal and spatial properties (Trait 4)—through the specialised methodologies developed in this thesis, especially when combined with auxiliary information (Traits 9 and 10), allows for a relatively robust preliminary understanding of the broader system.

However, a significant portion of essential system characteristics—specifically the internal and external dynamics and causal mechanisms governing the transfer of matter, energy, and genetic material (Traits 1–3)—are likely to be unique to each geobiome. These traits are less predictable from the others and therefore require dedicated, often multidisciplinary, investigation to uncover.

In summary, while the development of a methodological framework to empirically distinguish Bretskyan units in space and/or time and to infer their hierarchical relationships is a crucial step, such a framework can only offer a preliminary and coarse-grained understanding and categorisation of the systems it detects.

1.3.7. Defining Bretskyan Entities from Empirical Data: Key Observables, Spatial Properties and Limitations

For the successful development of an effective methodological framework for identifying and recognising units of the Bretskyan hierarchy, it is essential to consider which observables are most instrumental for their preliminary and practical detection and characterisation. The argumentation here is that these key observables are taxonomic occurrences and abundances.

Bretskyan hierarchy theory predicts that each geobiomic unit within the hierarchy should exhibit a unique taxonomic composition. Therefore, as elaborated in the Triadic Approach to Bretskyan Hierarchy section, the distinction and characterisation of these units should be grounded in taxonomic information. This is justified not only because taxonomic data reflect species composition, but also because they are embedded in rich, well-established bodies of knowledge—including ecology, phylogeny, and biogeography—which collectively provide insights into system-level processes.

In addition, taxonomic information captures the effects of spatial compartmentalisation imposed by dispersal barriers. Such compartmentalisation isolates biotic components spatially, shaping the set of possible ecological interactions and, consequently, the trajectories of coevolution. At the same time, it partitions the flow of genealogical information, which becomes reflected in the taxonomic composition of the biota. Over time, this leads to increasing taxonomic divergence between biotas that were previously connected but have become separated by dispersal barriers.

Thus, distinct taxonomic associations are key indicators for distinguishing Bretskyan units—particularly those operating at spatial and temporal scales sufficient for evolutionary divergence to occur. In practice, the primary observable for detecting geobiomic units is the occurrence of taxa, whether drawn from fossil records or contemporary ecological observation databases.

However, at shorter timescales—less than the typical species lifespan (e.g. ~1 Ma; Žliobaitė & Fortelius, 2022)—at smaller spatial scales (i.e. below the average species' geographical range), or in the presence of weaker dispersal barriers, taxonomic compositions may remain similar between geobiomes that are only loosely connected or were separated relatively recently. In such cases, differences are more likely to accumulate at the level of populations and communities, as demonstrated by macroecological evidence (Brown, 1995).

This divergence is expected to result from locally varying environmental conditions and ecological interactions, as well as from differing histories of ecological events that shape community composition over time. Accordingly, smaller-scale or more weakly disconnected geobiomes may be revealed not through taxonomic differences alone, but through analyses of species abundance patterns and community structure. Therefore, species abundance represents a critical observable and a valuable object of study in the detection and characterisation of such geobiomes.

Geobiomes also exhibit a distinctive topological property: they must be spatiotemporally contiguous. Although they may contain other, embedded geobiomes (i.e. topological holes)—such as terrestrial geobiomes nested within oceanic ones—their outer spatiotemporal boundaries must form a continuous whole. This requirement arises from the fact that geobiomes are characterised by discrete birth and death events, with their individuation (i.e. origin and persistence) resulting from the forced spatial compartmentalisation of taxa by surrounding dispersal barriers. These barriers create conditions for ecological integration and coevolution among compartmentalised taxa through spatial proximity and sustained cohabitation.

In this context, dispersal barriers are the primary drivers of spatial contiguity, as they define the extent and cohesion of geobiomes in space. The practical implication of this topological constraint is that any methodological framework designed to recognise units of the Bretskyan hierarchy must be capable of delineating spatially and temporally contiguous areas in which taxonomic associations, populations, or communities—whether inferred from occurrence or abundance data—are internally more homogeneous and externally more distinct from each other.

A practical nuance arises from the fact that what constitutes a dispersal barrier for one group of taxa may serve as a habitat for another (e.g. oceans for terrestrial taxa versus aquatic taxa). Consequently, the reconstruction of geobiomes for taxa associated with fundamentally different habitats (e.g. terrestrial versus marine) should be approached as separate endeavours.

Also, when considering the integration of distinct geobiomes into higher-tier geobiomes—for example, two continents separated by an ocean that nonetheless exhibit meaningful biotic or abiotic interactions (see section Example of Bretskyan Hierarchy)—it is important that the dispersal barrier (in this case, the ocean) be included within the spatial extent of the higher-tier geobiome. This inclusion is essential to uphold the principle of spatial contiguity—a defining characteristic of geobiomes, or any physical entity (i.e. patches in patch hierarchy). Since all interactions within a system are mediated through spatial coupling, a geobiome must be spatially contiguous in order to fully encompass the interactions that define and sustain its internal organisation. Also, the inclusion is warranted by the fact that dispersal barriers are integral components of, the higher-tier geobiome that encompasses the interacting systems since any interaction between such lower-tier geobiomes (e.g. continents) occurs via the physical flows of matter and energy across the dispersal barriers that separate them. Paradoxically, strong dispersal barriers act as connectors of large-scale geobiomes when viewed at the scale of the Gaia geobiome, as they mediate interactions and flows that integrate otherwise separate systems.

This methodological approach implies that higher-tier, loosely integrated marine and continental geobiomes will spatially overlap to some extent (e.g. Atlantic marine geobiome will overlap New World + Old World geobiome). This also means that Bretskyan hierarchy itself has such spatially overlapping nature, at least in two-dimensional projections of geobiomes. This spatial overlap reflects the multidimensional and habitat-specific nature of geobiomic organisation and underscores the need for habitat-specific delineation in lower-tier geobiome reconstruction.

Bretskyan vs. Bretskyan-like Hierarchy:

Crucially, spatially and temporally contiguous areas of relatively uniform taxic composition are only loosely related to the more holistic concept of geobiomes as integrated systems of matter, energy, and information transfer. Although these areas may align with geobiomes to some extent in space and time, they do not reveal how such systems function. Areas defined solely by taxonomic uniformity may, in fact, better correspond to the classical definitions of bioregions or related concepts in biostratigraphy and biogeography—such as biotic provinces, realms, ecological regions, biozones, or ecozones.

Distinguished bioregions are typically the product of bioregionalisation procedures, which often rely on varied and loosely defined criteria (Brocklehurst & Fröbisch, 2018; Denelle et al., 2025). Unlike geobiomes, bioregions are not always considered to have a temporal dimension, and not all authors or methodological frameworks treat spatial contiguity as a defining property. Nevertheless, some approaches and studies do incorporate both temporal span and spatial continuity in the definition of bioregions (e.g. Brocklehurst & Fröbisch, 2018).

The earliest formal delineations of bioregions can be traced back to the works of Sclater (1858) and Wallace (1876). For example, A. R. Wallace's definition of biogeographic realms: "Zoological regions are those primary divisions of the earth's surface of approximately continental extent, which are characterized by distinct assemblages of animal types." (1894, p. 613). Delineated bioregions (including Wallace's realms) are often arranged in nested hierarchical schemes, with increasingly dissimilar taxa defining higher-level bioregions (e.g. Brocklehurst & Fröbisch, 2018; Denelle et al., 2025; Gibert et al., 2022).

What is more, different taxa—especially in deep-time studies—are unequally represented in empirical datasets due to various biases, including sampling effort, sampling difficulty, preservation potential, and other taphonomic or methodological factors (Antell et al., 2024). For this and other reasons more related to research problems and goals, bioregionalisation studies often restrict their scope to selected groups of taxa (e.g. mammals, birds, or plants). As already discussed in the Practical and Methodological Implications subsection of the Dispersal Barriers section, such taxonomic exclusions or misrepresentations can result in substantial deviations between empirically detected bioregions and the idealised geobiomes of Bretskyan hierarchy, which—by definition—include all biota and thus should represent all taxa equally.

Furthermore, while taxonomic information reflects phylogenetic relationships, it does not faithfully capture system-level integration. In most cases, taxonomic patterns only indirectly reflect the integration or disruption of genealogical information flow—and often with a considerable delay, if at all. For example, if the temporal scale of the study is too narrow to accommodate speciation events, then taxonomic data will fail to reveal disruptions in genetic exchange, even if such disruptions have occurred.

A related issue is that taxonomic occurrence data alone are insufficient to detect small-scale geobiomes—such as those at the ecosystem or ecoregion level—when these are defined by weak or short-lived dispersal barriers, particularly those lasting less than the typical lifespan of a species. Additionally, there is likely to be a delay in the taxonomic response to geobiome fusion and fission events. This delay is likely to be exacerbated in cases where a fission event is immediately followed by a fusion event involving taxonomically distinct geobiomes. This occurs because taxonomic similarities take time to decline following a geobiome split, and likewise require time to increase following a merger.

The magnitude of this delay is likely influenced by three factors: (1) rates of speciation and extinction; (2) the degree and nature of changes in dispersal barrier permeability that led to geobiome separation or integration; and (3) the initial taxonomic (dis)similarities between the geobiomes involved. Thus, if the taxonomies of the split geobiomes were initially very similar, and the subsequent merger event—integrating these with other geobiomes—was weak (i.e. facilitated by only a mild to moderate increase in dispersal barrier permeability), then evidence of the merger and the formation of a higher-tier geobiome, as inferred from bulk changes in taxonomic occurrence associations, is likely to be considerably delayed. As a result, the delineated bioregions would reflect historical connections rather than the presence of newly formed geobiomic systems.

An illustrative example is the Great American Biotic Interchange (GABI), which began as early as 9 Ma with highly selective dispersals involving only a limited subset of taxa (Morgan, 2005). Larger pulses of faunal exchange occurred much later, between 3 and 1 Ma, following tectonic uplift associated with the convergence of the Caribbean and South American plates. This led to the formation of a volcanic arc and, ultimately, the Isthmus of Panama, which was significantly expanded during Quaternary glaciations due to sea level regression, thereby facilitating major interchange events (Cione et al., 2015). Similar patterns are evident in other historical biogeographic studies (e.g. cases in Halliday et al., 2020).

Collectively, these examples suggest that early stages of geobiome integration are likely to be marked by relatively subtle shifts in taxonomic composition. These nuanced distinctions between geobiomes and bioregions—particularly those defined solely by spatiotemporally contiguous taxic associations—underscore that the two are fundamentally different concepts.

Thus, geobiomes and their underlying characteristics cannot be directly observed through the spatial distribution of fossil records or recent occurrences. At best, we can infer the spatiotemporal extent of geobiomes from spatiotemporally contiguous, stable taxonomic associations—i.e. taxonomically defined bioregions. A spatially coherent association of taxa implies cohabitation, which in turn suggests ecological integration, potential coevolution, and ultimately—belonging to the same Bretskyan system.

While the concept of bioregions is not new to science, Bretskyan hierarchy theory proposes that bioregions should exhibit additional, informative traits beyond being merely stable aggregations of taxa localised in space and time. However, as discussed above, the correlation between contiguous, taxonomically established bioregions and Bretskyan geobiomes is far from perfect. It is essential to recognise the differences between the results produced by standard bioregionalisation methods and those emerging from interpretation within the framework of Bretskyan hierarchy theory.

Crucially, this recognition leads to the understanding that empirically derived nested hierarchies of taxonomically established bioregions and the hierarchies of Bretskyan geobiomes are fundamentally distinct. The former constitutes an empirical compositional hierarchy, which—within the framework of this thesis—is referred to as a Bretskyan-like hierarchy. The latter, by contrast, is an ontological, hybrid compositional and control hierarchy, exhibiting anastomosing structure that reflects both the physical integration of biotic components and the flow of matter, energy, and information.

The fact that bioregions and Bretskyan-like hierarchies are empirical in nature means they are shaped by the limitations of our observations—such as sampling biases, preservation constraints, and taxonomic resolution. Their lack of a control component also implies that their definitions do not directly depend on the presence of biotic and abiotic interactions, or on the transfer of energy, matter, and genealogical information. Just as ecological and genealogical process hierarchies influence and shape the Linnaean taxonomic hierarchy (Eldredge, 1985; Eldredge & Salthe, 1984), so too does the Bretskyan hierarchy shape and constrain the empirical, compositional hierarchy of bioregions.

Accordingly, the empirical compositional hierarchy of bioregions—the Bretskyan-like hierarchy—can be viewed as a proxy for the underlying Bretskyan hierarchy of geobiomes. In the early stages of geobiome research, the delineation of geobiomes in space and time and their placement within a nested hierarchical framework should be the primary focus. Thus, these nested empirical hierarchies serve as valuable preliminary approximations of geobiome systematics.

However, the emergence of true geobiomic systems depends on the assembly of integrated structures composed of biotic and abiotic interactions. Consequently, a critical component of geobiome research must involve the characterisation of these directly unobservable structures—namely, the pathways and modes of energy, matter, and genealogical information transfer, as well as the emergent macroscopic properties they produce. Multidisciplinary studies that focus on the functions, intensities, and actors involved in such biotic and abiotic interactions—and on the dispersal barriers operating within and between empirically derived geobiomes—are essential for validating and refining geobiome systematics. This process is analogous to how methods such as historical biogeography, stratocladistics, comparative morphology, and phylogenomics contribute to the validation and revision of the Linnaean taxonomic hierarchy.

Such studies are also necessary for advancing our understanding of fundamental aspects of geobiomes, including their functional properties, internal dynamics, and the relationships among different hierarchical tiers (see Triadic Approach to Bretskyan Hierarchy). Therefore, Bretskyan-like hierarchical units—bioregions—can only be interpreted as true geobiomes when supported by a strong body of evidence.

For example, such an interpretation is justified when boundaries correspond to known, strong spatial or temporal dispersal barriers that likely apply to a broad range of biota (not just the taxa under study), when taxonomic differences between bioregions are large and statistically significant, and when subsequent studies confirm the existence of compartmentalised systems with functional and genealogical integration.

From Anastomosing to Diachronic

Many nested compositional hierarchies in the material world exhibit strict part–whole relationships, in which each component is nested within a single higher-level system (e.g. Eldredge, 1985; Salthe, 1985). This perspective is valuable, as it greatly simplifies the analysis of hierarchical systems. However, such strict part–whole relationships are relatively rare in nature, and by extension, in real-world hierarchies. The smaller and more mobile a component is, the more frequently it is likely to change its position within the hierarchy.

Bretskyan hierarchy theory acknowledges this complexity. Its anastomosing, nested pattern accommodates varying degrees of part–whole strictness, depending on the temporal and spatial scale of observation. At very short timescales (e.g. temporal snapshots), or when smaller, more dynamic units are excluded, the Bretskyan hierarchy approximates a strict part–whole relationship and forms a properly nested hierarchical structure. However, when the temporal span is sufficient to allow for mobility, or when mobile small-scale units are included, the same unit may merge with or split from others multiple times, thereby altering its membership and position within the hierarchy. Examples include: pathogens spreading from one host to another in the case of smaller holobionts nested within larger holobionts; migratory birds moving between continents in the context of holobionts within geobiomes; and land bridges or large landmasses intermittently connecting two continents in the case of geobiomes nested within broader geobiomes. Each of these cases is resolved within Bretskyan hierarchy theory through its anastomosing design.

In practical applications, however, especially where empirical data are imperfect and fragmentary, resolving such dynamic membership changes at the smallest scales becomes analytically intractable. The temporal framework of a given study—and the completeness of the data—therefore determines which aspects of hierarchical dynamics can be meaningfully captured. For example, fossil data typically reveal only the location of preservation, not the full extent of where an organism lived or moved. As a result, small-scale geobiomes (e.g. ecosystem-sized units) in most cases cannot be reliably reconstructed—even with ideal, explicitly spatiotemporal bioregionalisation methods and ideal absolute dating of fossils—along with their fluctuating boundaries, nesting relationships, and trajectories.

When temporally static bioregionalisation approaches—such as those developed in this thesis (hespdiv) or other widely used methods discussed in the third chapter of the thesis—are applied to data spanning a time interval, any anastomosing pattern that may have occurred within that interval is effectively averaged out, producing units at the given (epoch) time scale. A static, strictly nested hierarchical structure is thus imposed on a dynamic system characterised by shifting memberships. The resulting Bretskyan-like hierarchy is diachronic sensu Nakajima (2004).

This has several implications for the properties of the resulting diachronic Bretskyan-like hierarchy:

1. The longer the temporal span of the study, the more diachronic the taxonomic composition of each unit will be.
2. Taxonomic similarity between units will tend to increase.
3. Boundaries between units will appear increasingly fuzzy.
4. A unit corresponding to a geobiome that was nested within several larger geobiomes during the study interval will, in the diachronic hierarchy, be nested within the unit it occupied for the longest period (assuming unbiased data and proper higher-tier unit reconstruction).
5. Similarity between any two units will be higher the longer the geobiomes they represent shared the same components, regardless of the sequence or frequency of changes in nesting structure.
6. Shared taxa between two units may result either from fluctuating dispersal barrier permeability or selectivity (indicating changes in nesting structure), or from the absence of dispersal barriers for those taxa (indicating direct integration of those units). Distinguishing between these scenarios is crucial but requires independent data sources and approaches. If such information were available, a diachronic nested hierarchy could be reformulated as a diachronic heterarchy, where each unit could be nested within several other higher-tier units. Moreover, if the timing or at least sequence of nesting changes could also be resolved, the structure could potentially be transformed into more or less synchronic anastomosing hierarchy.
7. Units with minimal taxonomic overlap and well-defined, less-fuzzy boundaries should be least affected by the complications introduced by diachronic composition and dynamic nesting patterns. They are likely to reflect separate geobiomic systems with stable boundaries.

In light of these considerations, it is important to develop tools that enable the cross-comparison of Bretskyan-like units within a diachronic hierarchy featuring a static nesting structure, as well as to assess the degree of boundary fuzziness. These concerns were central to the development of the methodological framework presented in this thesis—specifically, the bioregion cross-comparison and the boundary and composition sensitivity analysis approaches implemented in the hespdiv section. They were also integral to the interpretation of the case study results. Not all bioregions and biostratigraphic zones identified were interpreted as geobiomes in the Case Studies section; only those that were most distinct, exhibited the most stable boundaries, and corresponded to known temporal or spatial dispersal barriers were treated as such.

1.4. Summary

This section has provided a comprehensive overview of the theoretical foundations that underpin the organization of biota in space and time, illuminating how structural complexity emerges from the interplay between physical (biotic or abiotic) entities and energy gradients under non-equilibrium conditions.

A key mechanism facilitating structural complexity is the spatial coupling of multiple co-located energy gradients and physical entities which enhance their interactions and dynamics. Such interactions drive cascades of energy transformations and the formation of nested, hierarchically structured, spatially contiguous physical entities - patches. Consequently, the natural world can be characterized by a mosaic-like dynamic structure composed of patches, each possessing internal similarity and responding more or less coherently to uniform gradients. Patchiness dynamics reflects not only the local generation and dissipation of energy gradients, cascading cross-scale interactions driven by spatial coupling and emergence as well as disintegration of patches, but also contingent, low-probability events and initial conditions that significantly shape the unique evolutionary trajectories of individual patches, their nested relationships, and entire patch mosaics.

Hierarchy theory provides a crucial framework for conceptualizing this complexity. It captures the nested compositional and control relationships among entities across scales, emphasizing the triadic, scale-dependent perspective inherent in complex systems. By highlighting entities as holons—simultaneously parts and wholes—the theory facilitates the understanding of cross-scale interactions and the significance of emergent properties. Within this context, Bretskyan hierarchy theory emerges as particularly valuable, integrating genealogical, ecological, and geophysical processes into a unified framework that explicitly accounts for both abiotic and biotic interactions. This theory's emphasis on spatiotemporal continuity, anastomosing nestedness, and flows of matter, energy and information aligns exceptionally well with empirical realities, providing robust guidelines for analysing patterns of biota organization. As such it was selected as primary framework in explicating spatial and temporal biota spatiotemporal organisation within this thesis, and further parts of it will serve as foundation in evaluating methods and their capacity to explore this organization, as well as interpreting the results.

The exploration of structural complexity and hierarchy theory has demonstrated that the organization of the natural world is fundamentally patch-based, dynamic, compositional, and nested much like the Bretskyan hierarchy. This patch-based topological organization, though vividly exemplified by biological systems, is not confined to them. Rather, it is a general property of systems composed of nested, interacting physical entities, observable throughout both biotic and abiotic contexts.

Consequently, the methodological approach proposed in the thesis fourth chapter, although explicitly designed for flexible delineation of geobiomes, inherently possesses a broader utility beyond the immediate biological context. By supporting diverse delineation criteria—such as structural coherence, energy gradient interactions, feedbacks, and compositional boundaries—this method could be adapted to delineate similar nested, compositional patch-based hierarchies across numerous natural systems. Given the universality of structural complexity discussed in the theoretical foundation, any hierarchical, real-world systems characterized by nested patch dynamics could potentially be delineated using this methodological framework, provided the method is flexibly configured to accommodate system-specific criteria and data types.

Thus, the generalizability and adaptability of the delineation method underscore its potential to facilitate deeper understanding and management not only of biological units like geobiomes, but also of abiotic entities—such as geological structures, atmospheric phenomena, or cosmological formations—that manifest similar hierarchical complexity and organisation. This flexibility aligns directly with the foundational principles outlined earlier, reinforcing the methodological robustness and expansive applicability of the thesis contributions.

This section also introduced a fundamental distinction between two types of hierarchical structures: the nested, diachronic, static, data-driven compositional hierarchies composed of bioregions—referred to here as Bretskyan-like—and the ontological, dynamic, anastomosing hierarchies of geobiomes central to Bretskyan hierarchy theory, which incorporate both compositional and control dimensions. The thesis further aimed to bridge the gap between these frameworks by examining the characteristic traits of Bretskyan-like hierarchies and identifying the conditions under which their constituent units can be meaningfully interpreted as geobiomes. Also, it was noted that large-scale loosely integrate terrestrial geobiomes should spatially overlap with marine geobiomes.

2. METHODS USED TO STUDY SPATIOTEMPORAL ORGANIZATION OF BIOTA

A wide array of methods has been developed to investigate various aspects of the spatial and temporal structuring of biota. This chapter of the thesis is the embodiment of the second thesis task (see Introduction). However, it is beyond the scope of this thesis to provide a comprehensive account of all such approaches, or to explore each in detail. Instead, this overview will focus on the methodologies most relevant to the aims and content of the thesis. This is not to suggest that only widely used or mainstream approaches will be considered; where appropriate, attention will also be given to less popular but potentially insightful or historically relevant alternatives.

The chapter is structured as follows: it begins by a review of methods for the detection and analysis of bioregions. Then it covers an alternative paradigm—boundary detection and analysis. Finally historical biogeography methods are explored, which provides means of interpreting temporal changes in spatial biotic structure, whether these are expressed through bioregions or through boundaries.

2.1. Bioregion Detection and Analysis Methods

2.1.1.Bioregionalization

Bioregionalisation refers both to the practice of delineating bioregions and to the study of the underlying concepts and methodologies used in this process. Within the field, several primary methodological frameworks have been established, alongside a range of less conventional approaches. The main approaches typically involve cluster analysis, network analysis, ordination analysis, or a combination of these techniques (Fig. 4). These will therefore be the focus of the following review. In addition, methods developed for the detection of areas of endemicity will be considered as well. Although these approaches are less commonly used, in certain cases areas of endemicity may correspond to Bretskyan units or offer complementary insights into the endemicity levels of bioregions identified through other methods.

In this section, all these methodologies will be examined, discussing their underlying principles, philosophical foundations, advantages and limitations, particularly in relation to their suitability for analysing data organised according to Bretskyan hierarchy principles. Much of this discussion regarding bioregionalization methods is based on previously published article (Daumantas & Spiridonov, 2024b). The following section (Bioregion Analysis Methods) will be dedicated to overview approaches that can be used to investigate various traits of already established bioregions.

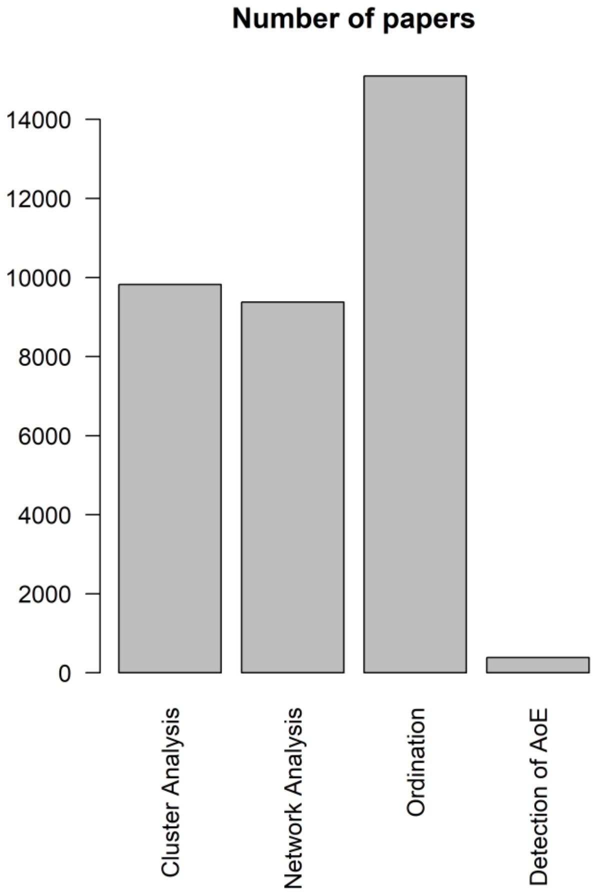


Figure 4. Number of Google Scholar search results (last checked on 8 April 2025) for the phrase '"X" "biogeography"'—where X is the method's name—restricted to publications from 2020 onwards. The restriction was used to reflect contemporary trends. The acronym AoE stands for areas of endemicity. The search phrase used for "Detection of AoE" was different, aggregating search results for three different methods: "biogeography" ("Endemicity analysis") OR ("parsimony analysis of endemicity") OR ("biotic element analysis").

Cluster Based Methods

Cluster analysis is a broad family of methods widely employed across various fields of data science (Davis, 2002; Jain et al., 1999; Kaufman & Rousseeuw, 1990). Its primary aim is to identify 'natural' groups (clusters) within a dataset. Because there are multiple ways to define these groups—and far too many potential groupings to exhaustively evaluate—various types of cluster analysis have emerged. They differ in how they search for clusters, the heuristics they adopt, whether they are hierarchical or non-hierarchical, and the types of clusters they detect (e.g. probabilistic versus categorical). For an example see Fig. 5.

Given that a comprehensive survey of every cluster analysis variant lies beyond the scope of this thesis, focus here will be on the most widely used traditional applications and their offshoots that may be used for uncovering spatiotemporal Bretskyan-like or more broadly patch-based hierarchical structures.

Hierarchical cluster analysis

Hierarchical cluster analysis is by far the most widely used form of cluster analysis (Jain et al., 1999). Although non-hierarchical approaches, such as the k-means method (MacQueen, 1967), are also common, their intrinsic lack of hierarchy makes them ill-suited for investigating patterns structured according to Bretskyan hierarchy principles. In hierarchical cluster analysis, a distance matrix between observations serves as input, and the output is a dendrogram illustrating both the hierarchical relationships among the detected clusters and the (dis)similarities between clusters at various levels of the hierarchy.

Depending on how clusters are identified—either from large clusters down to smaller ones, or vice versa—clustering techniques are classified as agglomerative or divisive. Agglomerative clustering follows a bottom–top approach: each observation initially forms its own cluster, and the two most similar clusters are iteratively merged until all observations are grouped into one root cluster. In this process, similarity between clusters is measured using a chosen linkage function (Kent et al., 2006). Multiple linkage functions exist (see Table 2 in Kreft and Jetz (2010) for summary), and the final results can vary markedly depending on which is selected (Davis, 2002; Kaufman & Rousseeuw, 1990).

By contrast, divisive clustering methods (e.g. the DIANA algorithm; Rousseeuw, 1990) implement a top–bottom approach. Rather than starting with each observation in its own cluster, the algorithm begins with a single cluster encompassing all observations and recursively splits it into two smaller clusters until, eventually, each observation is isolated as a singleton cluster.

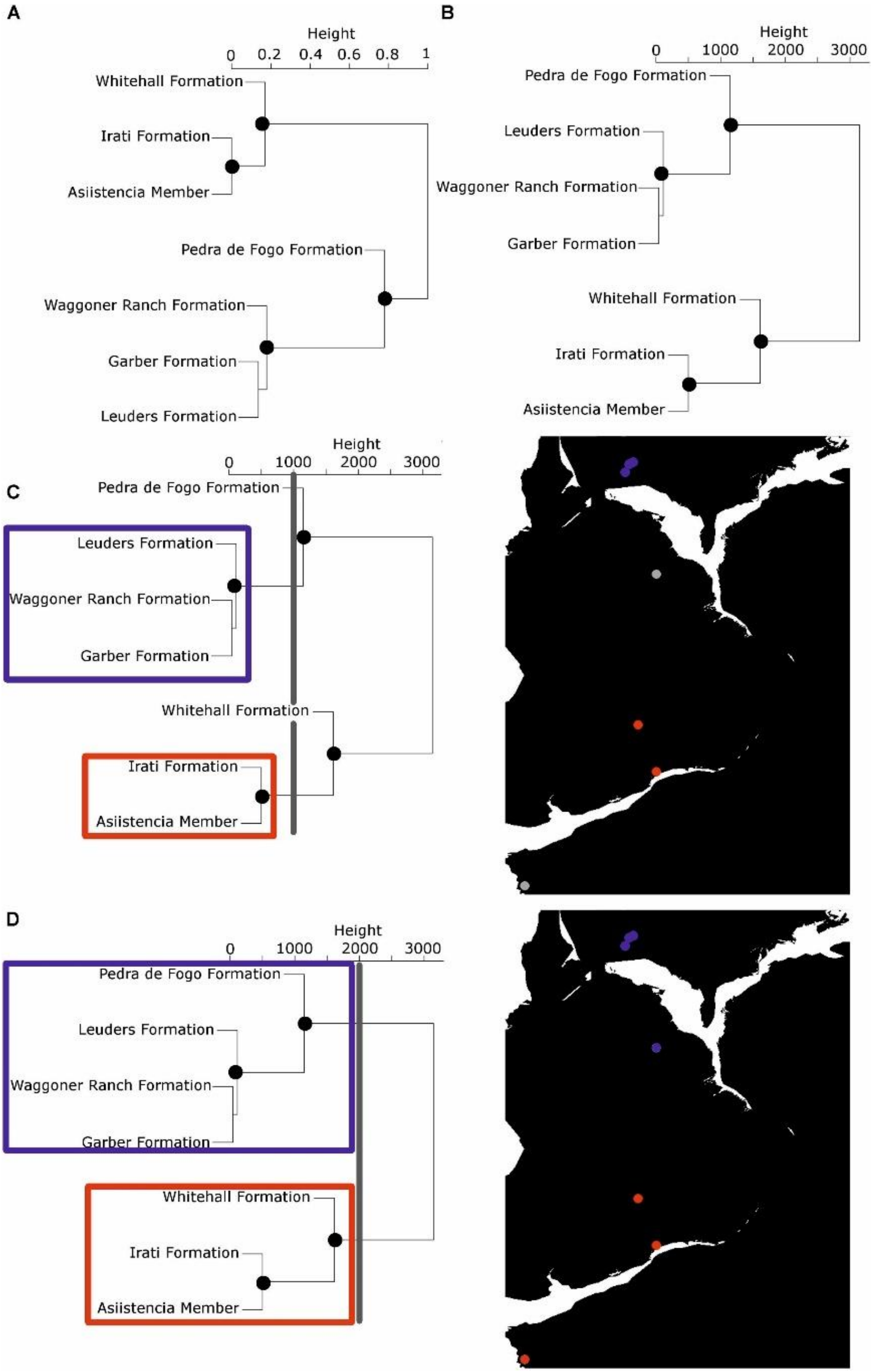


Figure 5. The example of various hierarchical cluster approaches using early Kungurian tetrapod data. (A) classical UPGMA dendrogram based on taxonomic dissimilarities between formations. (B) Dendrogram of the same

formations based on their pairwise geographic (Euclidean) distances (sometimes used bioregionalisation approach). Black nodes indicate shared clusters in both dendrograms, interpreted as spatially coherent areas of endemism (i.e., bioregions). (C, D) Visualisation of how geographic clustering scale influences bioregion definition following the method proposed in Brocklehurst and Fröbisch (2018). (C) With a clustering threshold of 1000 km, formations within that distance are grouped into four bioregions: two larger ones in palaeoequatorial North America (blue) and palaeotemperate South America (red), plus two isolated formations shown in grey. (D) At a broader spatial threshold of 2000 km, the formations are grouped into two bioregions, each encompassing broader palaeolatitudinal zones (blue = palaeoequatorial; red = palaeotemperate). Reproduced from Brocklehurst and Fröbisch (2018), licensed under CC BY 4.0 (http://creativecommons.org/licenses/by/4.0/).

Because there are exponentially many ways to partition observations (on the order of 2^N), heuristic procedures are necessary to maintain feasible computation times. In DIANA, for instance, the most distinct observation is placed in a “splinter group,” to which other observations are assigned if they are more similar to that splinter group than to the remaining observations; this process is repeated until all observations become singletons (Rousseeuw, 1990). Similarly, the bisecting k-means method applies the non-hierarchical k-means procedure recursively to generate two clusters at each step, stopping once a specified number of clusters is reached or another termination criterion is met (Steinbach, 2000).

Although both agglomerative and divisive clustering methods can reveal hierarchical structures in diverse datasets—including those capturing spatiotemporal taxonomic variation—they are not well suited to patch-based, Bretskyan-like hierarchies. Their principal limitation stems from defining clusters solely in terms of pairwise (dis)similarities between observations, without accounting for geographical spread or topology. Consequently, these methods do not guarantee spatially contiguous clusters—an essential property of Bretskyan entities (Fig. 6). Empirical research shows that enforcing spatial contiguity constraints commonly results in weaker cluster separation (Yuan et al., 2015); however, in the absence of such constraints, inevitably, the clusters produced will often lack spatial coherence. Moreover, because conventional clustering algorithms are not designed with explicit spatial analysis in mind, they generate groupings and hierarchical relationships (e.g. in dendrograms) but do not delineate the spatial boundaries of those clusters (i.e.

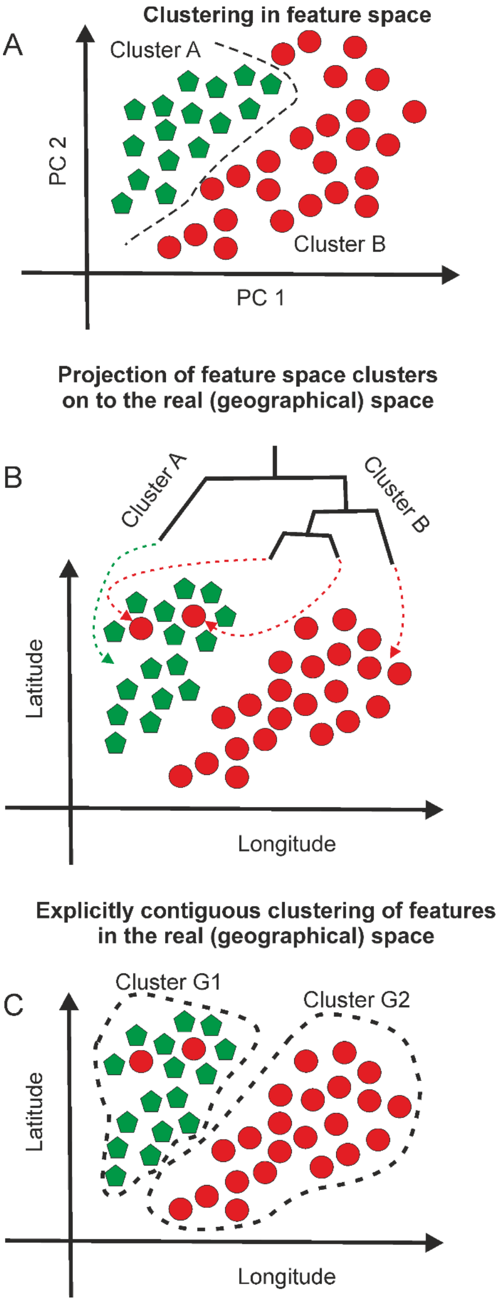


Figure 6. A) Cluster analysis conducted in feature space, such as the space of taxonomic compositions of palaeocommunities, groups or divides samples based solely on their similarities or differences, without accounting for their geographical positions. B) When these clusters are subsequently mapped onto geographical space, the resulting spatial representations are often non-contiguous, thereby violating the principles of spatially nested hierarchies. C)

In contrast, explicit spatial clustering partitions geographical space into contiguous regions by assessing differences in feature densities, ensuring both spatial contiguity and adherence to strict spatial subsetting hierarchies. Figure reproduced with permission from Daumantas and Spiridonov (2024b).

mathematically obtained lines that would envelope each cluster and separate them from each other in a map). Since geobiome boundaries often correspond to major dispersal barriers that follow large-scale topographical features (Spiridonov & Eldredge, 2024), they present a valuable focal point for studies employing suitably designed methodological approaches (e.g. Fortin, 1994; Kent et al., 2006; Oden et al., 1993). Indeed, a branch of spatial statistics specifically addresses the distribution of linear features in space (Davis, 2002) and boundary analysis (Fortin et al., 1996). Consequently, an ideal methodological framework for detecting and examining Bretskyan hierarchy patterns should not only group data and establish hierarchical relationships but also delineate spatial cluster boundaries.

Nevertheless, hierarchical clustering has traditionally been employed to generate taxonomic clusters that are then projected onto geographical space, despite the aforementioned limitations. For instance, Kreft and Jetz (2010) used this strategy to identify modern biogeographical regions, whereas Gibert et al. (2022) applied a similar approach to Old World Miocene mammals. Even so, both studies reported spatially non-contiguous clusters, more prominent at some subsamples or analysis levels: in Kreft and Jetz (2010), this occurred at the family level analysis, while in Gibert et al. (2022), some clusters overlapped to such an extent that establishing any spatially coherent entities was impossible. The likelihood of producing spatially non-contiguous clusters was observed to increase further down the cluster dendrogram.

The structure of the input data—specifically, a distance matrix between observations—also constrains the possibilities of hierarchical clustering methods and of other methods that operate on distance matrices (e.g. ordination analysis and network analysis). Crucially, sampling and preservation of the palaeontological record are highly heterogeneous in both space and time (Antell et al., 2024; Roger A. Close et al., 2020; R. A. Close et al., 2020; Foote & Sepkoski, 1999; Peters & Heim, 2010; Smith & McGowan, 2011; Wagner & Marcot, 2013). Consequently, the number of occurrences per locality often varies from a few to hundreds, and abundances per sample can range from a handful to thousands. Probability distributions of such data are typically right-skewed, with Lagerstätten localities occupying the far right tail and the mode occurring at low to intermediate species richness (e.g. Roden et al., 2020; Westrop & Adrain, 1998). When computing a locality-to-locality or sample-to-sample distance matrix, all sample-size information is lost, and each entry receives equal weight, irrespective of discrepancies in sample sizes and the amount of data each entry represents. This is problematic, given that most ecological similarity metrics are biased by sample size and diversity (albeit to differing degrees) (Alroy, 2015; Anne Chao et al., 2006; Wolda, 1981). As a result, clustering, ordination, and network methods delimit bioregions based on many biased pairwise comparisons, with small—and therefore typically more biased—samples exerting a disproportionately large influence on the outcome. Comparing pooled samples from putative bioregions would be more defensible; however, such an approach requires specifying the bioregions *a priori*, which is incompatible with the nature of clustering, ordination, and many network analyses.

Consider a hypothetical case in which (dis)similarity between clusters can only be measured meaningfully when there is a minimum required number of observations in each cluster. Such a situation might occur if the goal is to group observations based on differences between statistical models trained on these data, such as when attempting to reveal Simpson's paradox (Simpson, 1951), e.g. different model applies to different territorial or temporal subsamples. If a single location fails to meet the minimum observation threshold, it becomes necessary to group certain locations in advance or the analysis is impossible. However, this pregrouping process is non-trivial: hierarchical clustering cannot "undo" these initial groupings, and they introduce an artificial signal into the clustering results. This artificial signal can be challenging to disentangle from the true signal, complicating the interpretation of the results.

In palaeontological databases, especially for larger organisms, it is common to find localities with only a single occurrence. Although many ecological (dis)similarity metrics can mathematically compare a single-occurrence sample with those containing multiple occurrences, the outcomes of such comparisons are prone to various issues since most similarity metrices were originally designed to compare communities without considering the effects of sample size or diversity (A. Chao et al., 2006). Secondly, if single-occurrence samples dominate, comparisons using different metrics often produce near-identical (dis)similarity matrices. This happens because the comparison boils down to either "same taxon" or "different taxon," rendering the choice of (dis)similarity metric effectively meaningless (see example in Table 1). Consequently, localities with single occurrences must be pregrouped, which brings us back to the aforementioned problem of pregrouping influencing the clustering results.

Table 1. The choice of (dis)similarity metric has no discernible effect when applied to localities that contain only a single occurrence. (A) Presence–absence matrix illustrating hypothetical localities, each containing a single dinosaur genus occurrence. (B) The resulting similarity matrix of the data shown in A, computed using a variety of different similarity metrics (e.g. Sørensen, Jaccard, Morisita–Horn, or Bray–Curtis). This matrix was obtained using the "vegdist" function from the "vegan" package (Oksanen et al., 2007), with the "method" argument set to "chao", "altGower", "horn", "sorensen", "jaccard", "kulczynski", "bray", "clark", and "canberra". The use of other commonly known metrics, such as Euclidean, Manhattan, Raup–Crick, or Mountford, would produce a similar matrix containing only two distinct values—indicating either that localities share the same taxon or that they do not. As a result, in cases where primary data consist solely of single-occurrence localities, the choice of (dis)similarity metric has no effect on subsequent cluster analysis.

A)

Loc.\Genus	Ankylosaurus	Brachiosaurus	Diplodocus	Spinosaurus	Stegosaurus	Tyrannosaurus	Triceratops	Velociraptor
1	0	0	0	0	0	1	0	0
2	0	0	0	0	0	0	0	1
3	0	0	0	0	0	0	1	0
4	0	0	0	0	0	1	0	0
5	0	1	0	0	0	0	0	0
6	0	0	0	0	1	0	0	0
7	0	0	0	0	0	0	0	1
8	0	0	0	1	0	0	0	0
9	0	0	0	0	0	1	0	0
10	0	0	0	0	0	0	1	0
11	1	0	0	0	0	0	0	0
12	0	1	0	0	0	0	0	0
13	0	0	0	0	0	0	0	1
14	0	0	1	0	0	0	0	0
15	0	0	0	0	0	1	0	0

B)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
2	0													
3	0	0												
4	1	0	0											
5	0	0	0	0										
6	0	0	0	0	0									
7	0	1	0	0	0	0								
8	0	0	0	0	0	0	0							
9	1	0	0	1	0	0	0	0						
10	0	0	1	0	0	0	0	0	0					
11	0	0	0	0	0	0	0	0	0	0				
12	0	0	0	0	1	0	0	0	0	0	0			
13	0	1	0	0	0	0	1	0	0	0	0	0		
14	0	0	0	0	0	0	0	0	0	0	0	0	0	
15	1	0	0	1	0	0	0	0	1	0	0	0	0	0

Taking into account that various (dis)similarity metrics behave almost identically when comparing samples with a single occurrence, but diverge more noticeably as the number of occurrences increases, it follows that larger sample sizes lead each metric to function more consistently with its theoretical expectations (Wolda, 1981). Even in typical scenarios where localities contain a modest number of occurrences (e.g. 10–50), the influence of small samples can still be significant in masking the distinctiveness between different (dis)similarity metrics.

Since locality pregrouping introduces one set of challenges, and comparing small samples introduces another, traditional cluster analysis often struggles to exploit fully the varied perspectives offered by different (dis)similarity metrics without imposing artificial constraints on the results. This consideration also highlights the value of divisive clustering approaches, wherein data-partitioning algorithms can be designed to apply ecological (dis)similarity measurements internally for each tested pair of data subsets. By doing so, the initial splits—based on larger overall sample sizes—are measured more reliably, while only the final splits, which separate individual locations from one another, rely on the smaller sample sizes typical of agglomerative clustering algorithms. Regrettably, however, most divisive clustering approaches, such as DIANA, still rely on a precomputed sample-to-sample difference matrix and do not internally apply an ecological distance function to evaluate the performance of each subdivision. This limitation reduces their capacity to address issues arising from small sample sizes or to fully integrate ecological metrics into the clustering process.

Divisive clustering algorithms also have the potential to surpass agglomerative clustering algorithms in identifying the largest data clusters (Daumantas & Spiridonov, 2024b). The key difference lies in how they arrive at large-scale groupings. Agglomerative methods begin by treating each observation as its own cluster and then sequentially merge them, introducing multiple levels of irreversible decisions along the way. By the time they form a few large clusters, they have already made a substantial number of merging decisions—each of which can introduce errors that propagate upward through the hierarchy.

By contrast, divisive algorithms start with all observations in a single cluster and partition them step by step. To reach the same few large clusters, fewer subdivisions are required compared to the multiple merges executed by agglomerative methods. Consequently, the opportunity to accumulate—and thus propagate—errors is reduced. Empirical comparisons confirm that partitioning approaches (i.e. divisive algorithms) more frequently excel at capturing large-scale clusters (Burghardt et al., 2022; Roux, 2018), even though integrating ordination methods can also improve large-cluster detection in agglomerative approaches (Dommergues et al., 2009; Gibert et al., 2022). The advantage to detect large-scale patterns is particularly significant in palaeobiogeographical studies since large-scale features such as mountains play a defining role in shaping smaller-scale geomorphological features. These large features influence climate and hydrological systems, which in turn control the ecometric traits and taxonomic composition of palaeocommunities (Fortelius et al., 2016; Perrigo et al., 2020). Consequently, the largest compositional contrasts—and the highest hierarchical order structures — within biota are typically found at these broader spatial scales (Spiridonov et al., 2022; Spiridonov & Eldredge, 2024; Spiridonov & Lovejoy, 2022).

The final issue with traditional hierarchical clustering methods is that the distance between clusters—represented by the branching heights in the resulting dendrogram—does not reflect their true ecological distance. In agglomerative clustering, this height is determined by the chosen linkage function, which takes as input the precomputed sample-to-sample distance matrix (usually derived from ecological (dis)similarity metrics) and outputs a measure of inter-cluster distance based on these pairwise relations. Consequently, while there are many available linkage functions (e.g. see table 2 in Kreft & Jetz, (2010) for summary), none of them produce inter-cluster distances that are identical to those obtained by directly comparing two clusters using the original ecological (dis)similarity metric. Similarly, in the DIANA algorithm, the distances between clusters also derive from the initial sample-to-sample distance matrix. This rises a concern whether the clustering would remain the same, if true ecological distances would be used to define inter-cluster differences instead of linkage function outputs.

By contrast, methods like bisecting k-means do not require a precomputed sample-to-sample distance matrix, as they operate directly on a data matrix where rows represent observations (e.g., locations) and columns represent different numerical variables (e.g., taxa). However, these approaches are not based on well-established ecological (dis)similarity metrics; rather, they provide their own clustering perspective, comparable in this respect to agglomerative clustering methods that rely on linkage functions.

Summary of Limitations in Traditional Hierarchical Clustering

1. **No Guarantee of Spatial Contiguity.**

Traditional hierarchical clustering does not ensure spatially contiguous clusters, a requirement central to patch-based Bretskyan-like hierarchies.

2. **No spatial boundaries in the output.**

Traditional clustering approaches provide only data clusters and their relationships as depicted in a hierarchical dendrogram, without defining the spatial boundaries of these clusters. As a result, these boundaries have to be drawn on a map subjectively ‘by hand’ or using additional mathematical techniques such as computing a convex hull of cluster localities.

3. **Reliance on a Precomputed Sample-to-Sample Distance Matrix**

This introduces a set of problems and can necessitate the artificial grouping of samples from different localities, or force comparisons among undersized samples that skew the distance matrix.

4. **Branching Heights in Dendrograms vs. True Ecological Distances**

The distances between clusters shown in a dendrogram do not necessarily correspond to the (dis)similarity that would be obtained by directly applying the same ecological metric used to compute the initial input matrix.

Given these constraints, and considering the discussed performance differences between agglomerative and divisive clustering, an ideal methodological framework for capturing patch-based Bretskyan-like hierarchical structures should:

- Operate in a divisive manner,
- Output spatial cluster boundaries,
- Ensure spatial contiguity of clusters, and

- Internally incorporate ecological (dis)similarity functions to measure and express inter-cluster differences.

Now, let us proceed to a short overview of specialised offshoots of clustering methods designed explicitly for spatial data clustering.

Spatially Constrained Cluster Analysis Methods

Numerous contexts require the identification of spatially contiguous data clusters (Duque et al., 2007; Yuan et al., 2019; Yuan et al., 2015). Consequently, it is unsurprising that a variety of cluster analysis adaptations have been designed to meet this spatial contiguity requirement. For an in-depth overview, see Duque et al. (2007) and Aguilar Colmenero and Portela Garcia-Miguel (2024), as well as the references cited therein. In the present subsection, the focus will be on the generalised algorithm for enforcing spatial contiguity constraints in cluster analysis, as introduced by Legendre and Legendre (2012b), together with two relatively recent spatially constrained clustering approaches developed specifically for palaeobiogeographical studies (Brocklehurst & Fröbisch, 2018; Button et al., 2017).

General Spatially Constrained Hierarchical Clustering

A straightforward yet elegant algorithm for spatially constrained hierarchical clustering is outlined by Legendre and Legendre (2012). Its central principle is to maximise the distance (or dissimilarity) between observations that are not spatial neighbours. Consequently, the process consists of two main tasks: (1) identifying spatial adjacency, and (2) adjusting pairwise distances or similarities based on whether observations are spatially adjacent.

In the Legendre and Legendre (2012) algorithm, spatial adjacency is determined using Delaunay triangulation (Delaunay, 1934; Preparata & Shamos, 2012). Within a Delaunay triangulation, points in a plane are connected only if their respective Voronoi (Thiessen or Dirichlet) polygons share a boundary. Each Thiessen polygon defines a zone of influence around a particular point, encompassing all locations closer to that point than to any other. Thus, tessellation—the subdivision of space using Thiessen polygons—offers a natural approach for partitioning the study area, because the boundaries lie exactly at the equidistant locations between each pair of points. On this basis, using Delaunay triangulation to identify which observations are spatially adjacent is highly suitable for clustering tasks.

The second step involves integrating spatial adjacency with an ecological similarity or distance measure. According to Legendre and Legendre (2012), the Delaunay triangulation outcomes are encoded in a spatial contiguity matrix, where zeros and ones indicate whether a pair of observations are neighbours (initially, each observation represents its own cluster). A similarity matrix is then generated using conventional ecological similarity (or distance) metrics (e.g. Sorensen–Dice, Jaccard, Raup–Crick, or Euclidean distance). Next, the spatial contiguity matrix and the similarity matrix undergo a Hadamard product (element-wise multiplication), which zeroes out the similarity values for any non-adjacent observations.

Observations that emerge as most similar in the resulting matrix are grouped to form spatially contiguous clusters. After each such grouping, the spatial contiguity matrix is updated to reflect the newly formed clusters. The similarities between clusters are recalculated as well via the approach of general agglomerative clustering model which equitable to the application of a chosen linkage function (Legendre & Legendre, 2012b), and the Hadamard product is repeated between the two resulting matrices. Because spatially disjoint clusters effectively have zero similarity, they remain unmerged, thus preserving spatial contiguity in the final solution. A similar principle applies to k-means-based methods, which can be modified to include contiguity constraints (Legendre & Legendre, 2012).

Although this approach resolves the issue of spatial contiguity, the other three limitations of traditional hierarchical clustering methods—outlined in the previous subsection—persist.

Recent Cluster-based approaches in palaeobiogeography

In recent years, Button et al. (2017) and Brocklehurst and Fröbisch (2018) have applied novel spatially constrained clustering methods to palaeobiogeographical studies. Although these methods successfully yield spatially contiguous, non-overlapping clusters, several important challenges remain unsolved.

Button et al.'s approach is relatively straightforward: it applies k-means clustering to the palaeocoordinates of localities. As a result, the generated "bioregions" capture purely geographical distributions but do not incorporate any taxonomic information. Essentially, the method presupposes that multiple nearby localities share a homogeneous taxonomic composition, reflecting a single regional environment without dispersal barriers. While this assumption may hold for small clusters on different continent sides, in more uniformly sampled contexts, the outcome is likely to be trivial groupings. Moreover, given that the spatial distribution of localities can be significantly affected by uneven sampling patterns (Antell et al., 2024), the resulting bioregions can be biased accordingly.

The Brocklehurst and Fröbisch (2018) propose a two-stage hierarchical clustering scheme to ensure both spatial contiguity and taxonomic coherence (Fig. 5). The first analysis determines spatial clusters by measuring Euclidean distances among localities' palaeocoordinates, then cutting the resulting dendrogram at a chosen level to yield clusters of the desired spatial scale. The second analysis applies conventional hierarchical clustering to taxonomic distance matrices. Bioregions are defined as those spatial clusters that also align with the taxonomic clusters. Unlike the method of Legendre and Legendre (2012b) which modifies both the input distance matrix and the clustering procedure to enforce contiguity, Brocklehurst and Fröbisch's approach combines the outputs of two separate, standard cluster analyses. However, while it addresses spatial contiguity, it retains the limitations inherent in precomputed distance matrices. For instance, in their study, localities were pre-grouped by formation to avoid singletons, and formations with a single taxon were removed altogether, indicating that reliance on a precomputed sample-to-sample distance matrix can still necessitate the subjective data manipulation and compromise the method's general applicability. Also, the method mandates the choice of a spatial scale. While in some cases being able to investigate a specific scale can be a bonus, in most cases a general, scale-free solution is the desired outcome.

In conclusion, traditional cluster analysis methods—including their spatially constrained variants—remain popular tools for bioregion identification but still exhibit significant limitations when applied to Bretskyan hierarchy patterns. Even though spatially constrained approaches can enforce topological contiguity, they often lack explicit spatial boundaries, do not guarantee that dendrogram branch lengths reflect genuine ecological distances, and generally depend on precomputed sample-to-sample distance matrices, which can introduce additional complexities or biases.

One reason for the prevalence of these agglomerative clustering algorithms may be their relatively light computational requirements, which were especially advantageous during periods of more limited computer power (Legendre & Legendre, 2012a). However, given modern technological capabilities, computational constraints no longer necessarily dictate algorithmic choices, opening opportunities for more sophisticated methods that could address many of the issues outlined above. Ultimately, refining or developing new spatially constrained clustering approaches capable of defining spatial boundaries, preserving spatial contiguity, and accurately capturing ecological relationships would significantly improve the applicability of clustering analyses to Bretskyan hierarchy investigations.

Ordination Based Methods

The central principle of ordination methods is to arrange observations (or variables) along reference axes according to their (dis)similarities (Davis, 2002; Legendre & Legendre, 2012a). Although these methods do not explicitly produce a classification—hierarchical or otherwise—they are remarkably effective at highlighting principal gradients within the dataset, clarifying how observations vary along these gradients, and thus revealing the underlying data organisation (Fig. 7). They can detect clusters of similar observations, pinpoint directions of gradual change, differentiate between discontinuous and continuous data variation, and determine which variables drive the observed patterns. As a result, ordination offers a distinct and complementary perspective on the spatiotemporal organisation of biota, explaining why numerous studies integrate ordination with other exploratory approaches, including cluster or network analyses (Gibert et al., 2022; Jattiot et al., 2018; Neige et al., 2021; Pelletier, 2021; Penn-Clarke & Harper, 2021). This complementary role, combined with its explanatory power, likely accounts for the widespread popularity of ordination in bioregionalisation studies (Fig. 4). Since ordination results can be post-processed to infer or delineate bioregions, ordination analysis is considered here as one of the key methods in bioregionalisation.

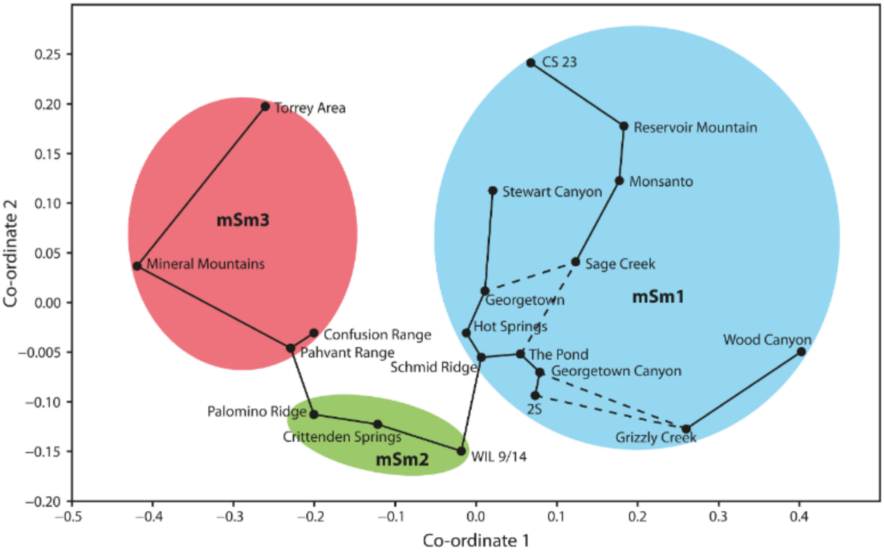


Figure 7. Example of ordination method (non-metric multidimensional scaling, NMDS) applied for bioregionalisation purposes on ammonoid faunas from Early Triassic, Western USA Basin. Most frequently recovered NMDS configuration (appearing in 378 out of 500 iterations, or 75%) shown with a

superimposed minimum spanning tree. The Kruskal stress value for the ordination is 0.18. Dashed lines indicate areas where variation across NMDS iterations was not statistically significant. Reproduced with permission from Jattiot et al. (2018).

The mathematical underpinnings of ordination methods are generally more complex than those of cluster analyses, and a broad range of techniques fall under the ordination umbrella. Their fundamental principle is to identify orthogonal directions in the data that capture the greatest variation, while preserving distances between data points. Each new direction accounts for progressively less variation, and, in theory, the number of such principal directions can match the number of original variables. However, only a small number of these directions (often two or three) are typically needed to explain most of the variation. As a result, ordination methods not only expose the underlying data structure but also reduce its dimensionality.

Furthermore, because the principal directions are orthogonal, they can be particularly valuable when subsequent analyses require the assumption of variable independence (i.e. no multicollinearity). Each principal direction, representing a substantial portion of the dataset's variation, often carries a meaningful interpretation—allowing for a more streamlined view of the data.

Principal Component Analysis (PCA)

For illustrative purposes, here is a concise explanation of Principal Component Analysis (PCA), one of the most widely used methods in the ordination family (Google search results for the phrase '"Principal Component Analysis" "biogeography"' returns even more results (16,400) than '"ordination" "biogeography"' (15,100)) (Legendre & Legendre, 2012a):

1. **Data Preparation**
    - Begin with a matrix A containing species counts from various sites (rows = sites, columns = species).
    - Subtract the mean (or otherwise standardise/centre) each column to produce a centred matrix X.
2. **Dispersion Matrix**
    - Pre-multiply X by its transpose and divide by (n−1) to obtain the variance-covariance matrix S:

$$S = \frac{X'X}{n-1}$$

Eq. 1

3. **Eigen-Decomposition**
    - Find the eigenvectors and eigenvalues of S by solving:

$$\left(S-\lambda_k I\right)u_k = 0$$

Eq. 2

In eq. 2, is identity matrix.

- Scale each eigenvector to unit length, forming the matrix U.

4. **Projection onto Principal Axes**
    - Multiply X by U to project observations into the space defined by the principal component axes.

By simplifying data into a smaller number of principal axes and ensuring orthogonality among them, PCA (and other ordination methods) can bring to light major patterns in the dataset while reducing redundancy and easing the interpretation of complex, high-dimensional data.

The eigenvalues indicate the amount of variation accounted for by each principal component, while the eigenvectors represent the loadings of individual variables onto those components. Interpreting these loadings is essential: large positive values signify a strong positive correlation with that component, whereas large negative values reflect a strong negative correlation. Although PCA relies on multiple assumptions about the dataset (e.g. Euclidean distances, linear relationships), more general ordination methods—such as non-metric multidimensional scaling (NMDS)—impose far fewer assumptions, offering greater flexibility in many ecological and palaeontological contexts. For example, the ordination can be directly applied to (dis)similarity matrix between sites, using methods like principal coordinates or NMDS (Gibert et al., 2022; Lefkovitch, 1976).

Ordination applications in exploring the organizational structure of palaeobiota

When ordination is applied to a taxonomic dataset's dispersion matrix, the resulting projection of sites within an ordination space—together with an examination of taxon loadings on the various axes—can provide a nuanced overview of how different biotic communities are distributed among the studied sites. Any taxonomic gradients or clusters present in the data may therefore become evident. Moreover, the relationships among sites, or groups of sites, tend to be more complex than those identified by cluster analysis, since each site's position relative to others can reveal more intricate interactions than the binary assignment of a site to a single cluster (Brayard et al., 2007).

Nevertheless, the “clusters” suggested by ordination space are effectively aggregations of sites in particular regions, rather than formal clusters labelled by a clustering algorithm. As a result, ordination methods, while capable of uncovering organisational structures in taxonomic datasets, do not inherently align with spatiotemporal Bretskyan hierarchies or other palaeobiogeographical constructs. In particular, they do not provide cluster labels, hierarchical relationships, or spatial boundaries that could be used to delineate bioregions on a map.

Although ordination techniques can be employed independently to examine taxonomical or morphological gradients among sites (e.g. Pelletier, 2021), palaeobiogeographical studies often deploy them alongside cluster analysis to gain deeper insights into interrelationships among clusters and to corroborate findings (Jattiot et al., 2018; Neige et al., 2021; Penn-Clarke & Harper, 2021). Such studies frequently use the same taxonomic (dis)similarity matrix for both the ordination and the clustering approach (e.g. Jattiot et al., 2018). The robustness of cluster analysis outcomes is commonly quantified via cophenetic correlation, which measures how closely distances among clusters mirror those among individual observations. Meanwhile, ordination results are evaluated using stress values, indicating how faithfully distances among observations in the ordination space represent their original distances.

A popular alternative is to combine cluster and ordination methods by conducting hierarchical clustering on principal components or coordinates, often referred to as HCPC (Gibert et al., 2022; Lefkovitch, 1976). In Gibert et al. (2022), HCPC outperformed conventional agglomerative hierarchical clustering (UPGMA) in identifying spatially contiguous mammal bioregions. However, even HCPC can occasionally fail to detect fully spatially coherent clusters, or may require reassigning some observations to different clusters to preserve contiguity (Gibert et al., 2022).

Ordination methods may also be combined with network analysis, for example, by overlaying sites (plotted in ordination space) with a minimal spanning tree (Brayard et al., 2007; Penn-Clarke & Harper, 2021). Because a minimal spanning tree can be subdivided hierarchically—for instance, by removing the k longest edges—clusters can be identified (Gower & Ross, 1969; Zahn, 1971). However, as with other approaches, spatial contiguity is not guaranteed because these operations are performed in data space rather than explicitly in geographical space (Fig. 6).

Summary of Limitations in Ordination Analysis

Although ordination methods differ considerably from cluster analysis in their technical application, underlying philosophy, and objectives, they share most of the limitations:

- They require additional methods to produce clusters.
- They do not provide spatial boundaries between clusters.
- They offer no guarantee of spatial contiguity.
- The distances between clusters in ordination space differ from the "true" ecological distances that would be obtained by applying the (dis)similarity metric directly to the clusters.
- As with cluster analysis, ordination demands either a sample-to-sample (dis)similarity matrix or a [site x taxon] matrix of abundance counts. This requirement can introduce issues such as pre-grouping or eliminating small samples, as well as sample-size bias. Also, it hampers analysis of datasets dominated by singletons.

Despite these constraints, ordination methods serve as an excellent exploratory tool, offering an alternative and complementary perspective on the spatiotemporal organisation of biotic communities. Since Bretskyan hierarchy theory and other compositional hierarchies rely on strictly nested hierarchical frameworks, standard hierarchical methods, such as cluster analysis, may overlook gradual changes within entities, as well as the intermediate positions of certain entities in a hierarchy (Brayard et al., 2007; Nakajima, 2004). Given the pervasive nature of spatial biotic gradients (Marcot et al., 2016; McCoy & Connor, 1980), using ordination in tandem with methods that expose hierarchical patterns can offer a more holistic understanding of the spatiotemporal organisation of biota.

Network Analysis Based Methods

Over the past two decades, network analysis (NA) methods have gained traction in palaeobiogeography, with a growing number of studies highlighting their advantages over more conventional cluster- and ordination-based approaches (Brayard et al., 2007; Button et al., 2017; Dera et al., 2011; Dunhill et al., 2016; Edler et al., 2016; Halliday et al., 2020; Huang et al., 2016; Kiel, 2017; Penn-Clarke & Harper, 2021; Rojas et al., 2017; Sidor et al., 2013; Viglietti et al., 2022; Vilhena & Antonelli, 2015).

In NA, entities (e.g. localities / bioregions, collections species, or higher taxonomic groups) and their pairwise relationships serve as the input. The analysis then produces a graph, where each node represents an entity and an edge signifies a significant relationship between two entities (Fig. 8). The graph layout—the specific arrangement of nodes and edges—depends on the algorithm used. In many implementations, nodes that possess numerous connections, are connected to groups of nodes, or exhibit many short connections, naturally gravitate towards the centre of the graph. By contrast, peripheral nodes tend to have fewer connections, longer edges, and typically belong to a single cluster.

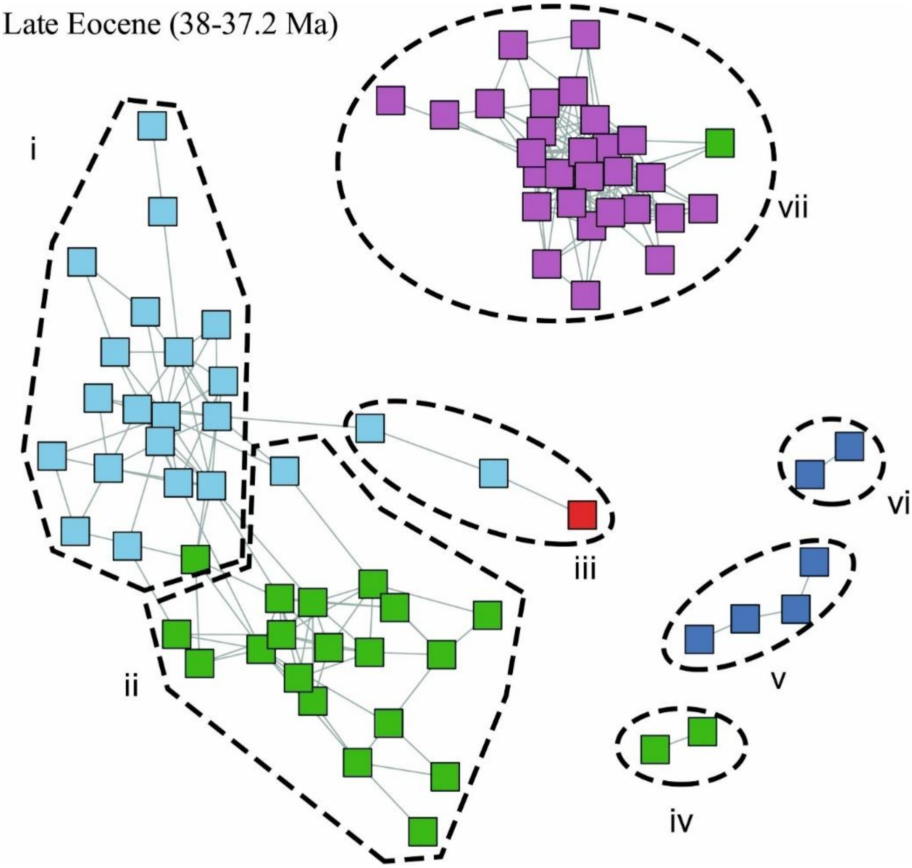


Figure 8. Example of network analysis output. Faunal similarity network of the Late Eocene vertebrate sites. The network reveals seven distinct clusters: (i) Asia together with the Pruett Formation (USA), (ii) North America alongside the Changxindian Formation (China), (iii) the Kuldana and Iwaki formations and the Shangqinglong fissure fill site, (iv) marine-associated formations (Jackson and Yazoo, USA), (v) Argentina, (vi) Peru, and (vii) Europe, including the Wind River Formation (USA). Continents are colour-coded as follows: North America – dark green, Asia – light blue, South America – navy blue, Europe – pink, Indian subcontinent – red, Madagascar – grey, Africa – orange, Australia and New Zealand – yellow, and Antarctica – pale green. Reproduced with permission from Halliday et al. (2020).

Commonly used graph layout algorithm in palaeobiogeography is based on simulation of physical forces between nodes (e.g. ForceAtlas2; Vilhena & Antonelli, 2015). In this algorithm nodes repel each other like charged particles while their edges serve as springs pulling connected nodes together, and pairwise interrelations determine how much these 'springs' can be stretched. Simulations of such simple physical interactions converges to stable optimal positions of nodes. Alternatively, when the primary interest lies in connections between nodes, and they represent geographical localities – as it is common in (palaeo)biogeography – graph is superimposed on the geographical map, with nodes placed on their geographical locations (e.g (Dera et al., 2011; Dunhill et al., 2016).

In network analysis (NA), the entities under study need not be of a single type, and edges can also take multiple forms. Given the inherently dual nature of biogeographical data—locations and taxa—one widely adopted strategy is to construct bipartite networks in which each node set represents, for example, localities and taxa (Button et al., 2017; Edler et al., 2016; Kiel, 2017; Rojas et al., 2017; Sidor et al., 2013; Vilhena & Antonelli, 2015), or taxa and collections (Huang et al., 2016). In this setup, the bipartite network can be represented by a bipartite adjacency matrix, split into two parts that capture taxa associations (e.g. number of co-occurrences) and taxonomic overlap between locations (e.g. number of shared taxa) (Vilhena & Antonelli, 2015). Data structured in this manner can be analysed directly using NA methods, thus avoiding the pre-processing of taxonomic data via ecological (dis)similarity metrics, preserving additional detail in the network and circumventing the biases commonly introduced by sample size, uneven sampling strategies, spatial scale, or assumptions about particular ecological metrics (Vilhena & Antonelli, 2015). Consequently, bipartite networks constructed from bipartite adjacency matrices often outperform unipartite networks based on (dis)similarity matrices (Edler et al., 2016; Vilhena & Antonelli, 2015). Nonetheless, using ecological (dis)similarity matrices to define relationships among nodes also remains a popular option, capable of yielding valuable insights (e.g. Halliday et al., 2020; Kiel, 2017).

Additionally, multiple types of edges can be introduced to capture different dimensions of the relationships among nodes. In Dunhill et al. (2016), for example, each node represented a landmass, with two categories of edges—one reflecting geographical connectivity (determined probabilistically by sea-level changes and the presence of seaways), and another indicating the number of shared dinosaurian families. In this design, two landmasses remain connected if they are geographically contiguous, even in the absence of shared taxa, drawing on the biogeographical assumption that contiguous landmasses generally exhibit higher taxonomic overlap than discontinuous ones.

Moreover, pairwise relationships among nodes can be expressed in several ways, ranging from traditional (dis)similarity metrics to co-occurrence counts or even phylogenetic distances between taxa from different localities. The latter method accommodates both taxonomic and geographic singletons (Button et al., 2017) thereby extending the applicability of network analysis to a broader range of datasets. As a result, NA stands out as a versatile framework, capable of supporting diverse research aims and experimental designs.

Identifying Clusters Within a Network

Although insightful palaeobiogeographical inferences can be made by exploring a network without dividing it into clusters (eg. Dunhill et al., 2016), obtaining bioregions from locality or locality–taxon networks typically requires network-based cluster analysis. Much like traditional clustering, network clustering offers both agglomerative and divisive variants, and—as in conventional cluster analyses—divisive approaches often outperform agglomerative ones since agglomerative methods tend to yield clusters made up only of nodes forming the "cores" of larger, more realistic clusters (Newman & Girvan, 2004).

Under the agglomerative paradigm, the general procedure is to add the strongest / shortest edges to the network incrementally until reaching a chosen stopping criterion. By contrast, divisive methods introduced by Newman and Girvan (2004) rely on edge betweenness—a property that reflects how frequently edges lie between different clusters of nodes. Crucially, this measure does not depend on the strength of a connection: for instance, an "island" between two continents might share substantial taxonomic similarity with both, leading to strong edges, yet it would exhibit high betweenness, indicating that removing those edges optimally separates the network.

Betweenness can be measured in different ways, forming a spectrum. At one end is shortest-path betweenness, which identifies all shortest (geodesic) paths connecting each pair of nodes and calculates how many such paths traverse a given edge. At the other end is random-walk betweenness, which envisions each pair of nodes as a source and sink, allowing a signal to travel randomly until it arrives at its destination. The betweenness of an edge is then assessed by counting how frequently signals pass through it. Ultimately, these measures span a range from strictly optimal paths to random ones (Newman & Girvan, 2004).

However, InfoMap (Rosvall & Bergstrom, 2008) is regarded by many authors as the best-performing network clustering algorithm, or at least strongly endorsed, in several comparative studies (Aguilar Colmenero & Portela Garcia-Miguel, 2024; Aldecoa & Marín, 2013; Edler et al., 2016; Fortunato, 2010; Rojas et al., 2017). Like the approaches described by (Newman & Girvan, 2004), InfoMap also simulates a random walk through the network. In this case, however, the walker's movements are probabilistically determined by edge weights, and directions, if the network is not unidirectional. Consequently, the random walker tends to loop within densely connected clusters of nodes, where the network's architecture supports more frequent local transitions.

InfoMap seeks to partition the network in such a way as to minimise the description length of the random walk path, encapsulated by the Map Equation (Rosvall & Bergstrom, 2008):

$$L(M) = qH(Q) + \sum p_i H(P_i)$$

Eq. 3

In Eq. 3, *L(M)* is the description length of the random walker's path through the network given the partition *M*; q is the probability that the walker switches between clusters; *H(Q)* is the entropy of switching between clusters; p_i – is the fraction of time the random walker spends in cluster *I*; $H(P_i)$ – is the entropy of the random walker's movement within cluster *i*.

Eq. 3 is composed of two key terms. The first, *qH(Q)*, reflects the information cost of inter-cluster movements. When the probability of cluster-switching (*q*) is high—especially in the presence of numerous clusters that share similar transition probabilities, resulting in elevated cluster-switching entropy (*H(Q)*)—the description length for movements between clusters becomes inflated. The second term, $\sum p_i H(P_i)$, captures the information cost of within-cluster movements. If the random walker spends prolonged periods in a certain cluster, and that cluster contains many nodes with relatively uniform interconnections, the term value for that cluster will be high, indicating that long description will be needed to code the movements of random walker within that cluster. Adding these two terms yields the total description length, *L(M)*. InfoMap aims to partition the network in such a way as to minimise L(M), thereby optimally reflecting the network's intrinsic community structure (Rosvall & Bergstrom, 2008).

Since it is computationally infeasible to evaluate all possible partitions of the network, InfoMap employs a greedy search algorithm that tests promising partitions, based on probabilistic estimates derived from the random walker's visit frequencies at each node. This procedure is further refined via a simulated annealing step (Rosvall & Bergstrom, 2008), ensuring that (sub)optimal partitions are explored and potentially improved to reach a globally superior partitioning.

In a manner analogous to ordination-based approaches, cluster analysis can also be combined with NA: one can still apply cluster analysis to derive clusters and then overlay these clusters on the network graph (Penn-Clarke & Harper, 2021), clarifying the relationships among clusters and localities. Consequently, NA provides a variety of distinct and often high-performing strategies for detecting bioregions or illuminating their interrelationships, whether clusters are defined within NA itself or by other methods.

Network Structure Metrics

Network analysis (NA) offers a variety of metrics to assess the structure of a network. Basic examples—such as centrality measures, clustering coefficients, modularity, and reciprocity—are reviewed in Newman (2018). Given the relatively recent emergence of NA methods, many novel or yet-to-be-discovered metrics may lie ahead. Indeed, new proposals such as the surprise index (Aldecoa & Marín, 2011) appear to outperform traditional measures. Moreover, the interpretation of each metric heavily depends on the underlying data and network design; in biogeographical networks, these metrics can capture and reflect various biogeographically meaningful processes and patterns (e.g. Dunhill et al., 2016). By contrast, there are far fewer metrics available for quantifying the structures detected by clustering-based or ordination-based methodologies (see, for example, Legendre and Legendre (2012a) for a limited discussion of measures like cophenetic correlation for clustering, or stress for ordination).

Summary of Advantages and Limitations in Network Analysis

Overall, network analysis (NA) stands out as a powerful analytical tool. Like ordination approaches, it preserves gradational information while offering a wide array of methods to identify and characterise clusters and their internal structures. The allocation of observations within a network is based not only on direct comparisons but also on higher-order associations, allowing for the detection of more complex relational patterns.

Unlike cluster and ordination methods, NA is not restricted to representing relationships between observations through a single pairwise (dis)similarity matrix. Instead, it can integrate a diverse range of data sources, including taxonomic co-occurrences, phylogenetic distances, and geographical connectivity, representing these relationships using different types of edges.

This flexibility allows NA to capture the multifaceted nature of biogeographical and palaeobiogeographical data.

Furthermore, NA can incorporate multiple types of entities within a single network. Bipartite locality–taxa networks effectively illustrate how NA can represent the dual nature of biogeographical data. This approach can be extended to create tri-partite age–locality–taxa networks, enabling a more comprehensive representation of the temporal, spatial, and taxonomic dimensions inherent in palaeobiogeographical data. Incorporating geographical connectivity as a criterion for establishing edges ensures the formation of spatiotemporally contiguous clusters. Given that hierarchical structures can also be identified within networks (Clauset et al., 2008), it means patch-based Bretskyan-like spatiotemporal hierarchical structures can be effectively detected and studied using NA.

The growing traction of NA in palaeobiogeography over the past couple of decades, with many authors highlighting the unique perspectives it offers compared to other methods (Brayard et al., 2007; Button et al., 2017; Dera et al., 2011; Dunhill et al., 2016; Edler et al., 2016; Halliday et al., 2020; Huang et al., 2016; Kiel, 2017; Penn-Clarke & Harper, 2021; Rojas et al., 2017; Sidor et al., 2013; Viglietti et al., 2022; Vilhena & Antonelli, 2015), might suggest that NA is the ultimate tool for analysing spatiotemporal biotic patterns. However, like all methodologies, NA comes with its own set of limitations. In fact, it shares several constraints with traditional methods. These limitations include:

1. **No spatial boundaries between clusters in the output.**

NA identifies clusters based on network structure but does not explicitly define spatial boundaries for these clusters, which is a key requirement or even the study object in some of the biogeographical studies (e.g. Fortin et al., 1996).

2. **Network links between clusters do not necessarily reflect "true" ecological distances.**

While network analysis (NA) offers a distinct perspective for identifying clusters and defining their relationships, the distances between clusters within a network do not always correspond to the (dis)similarities that would be measured directly using traditional ecological (dis)similarity functions. This discrepancy arises because higher-order associations within the network can link nodes or clusters that are, in fact, dissimilar in terms of shared taxa.

Although the inclusion of higher-order associations provides an additional layer of information, offering more nuanced insights into complex relational patterns, there are situations where it may be preferable to focus solely on representing direct (dis)similarities between clusters. In such cases, indirect associations might obscure (macro)ecological relationships, leading to misinterpretations of the biogeographical structure.

3. **Reliance on a precomputed sample-to-sample matrix**

Despite NA’s flexibility in accommodating different comparison measures—including those that can integrate singleton observations (e.g., phylogenetic distances, as demonstrated by Button et al. (2017))—it still fundamentally relies on pairwise comparisons. When traditional ecological (dis)similarity metrics are employed, a sample-to-sample (dis)similarity matrix is required as input. This introduces the same issues commonly encountered in ordination and cluster analysis, such as sample size biases and the necessity to eliminate or pregroup small samples. This pre-processing step determines the smallest spatial unit of analysis (e.g., locality, formation, bioregion, or landmass), which in turn determines the final results.

To conclude, the last two limitations highlight NA's inability to seamlessly integrate traditional ecological (dis)similarity metrics. While NA appears more flexible than clustering and ordination methods in how it measures and expresses relationships between observations and identifies clusters, its capacity to fully incorporate standard (dis)similarity metrics remains limited.

As a result, researchers recognising these constraints are often compelled to develop alternative approaches for representing pairwise relationships between nodes (Button et al., 2017). This is particularly unfortunate, given the numerous advantages of NA and the fact that ecological (dis)similarity metrics are well-established, extensively documented, and widely used in both ecological and palaeobiogeographical research.

Detection of Endemic Areas

Areas of endemicity—defined as regions that congruently and non-randomly encompass the geographical ranges of two or more taxa (Nihei, 2006)—are fundamental study objects in biogeography (Brian R. Rosen, 1988). Delineating areas of endemicity (used interchangeably with "endemic areas" here) can thus aid in understanding the spatial and temporal structuring of biota. Taxonomic relationships between these areas not only reflect environmental or ecological similarities but also may shed light on evolutionary biogeography (Brian R. Rosen, 1988). Accordingly, the methods discussed in this section—particularly parsimony analysis of endemicity—can be seen as overlapping with those reviewed in the section on historical biogeographical inference. Given this dual utility, despite their less mainstream status (Fig. 4), these approaches merit inclusion in this overview.

Biogeographical inferences become possible in analysis of endemic areas when applying a dynamic interpretation approach that examines taxonomic relationships between endemic areas over time (Nihei, 2006). For example, an increase in similarity between endemic areas could indicate a dispersal event, whereas a decline in similarity might suggest the formation of a dispersal barrier. However, static interpretations can also yield biogeographical insights in certain cases (Brian R. Rosen, 1988). For instance, congruent patterns in the relationships between endemic areas across multiple contemporary taxonomic groups—especially among groups with differing ecological niche requirements—may reflect the influence of historical geological events that led to the formation or removal of significant dispersal barriers (Rosen & Smith, 1988).

However, the question remains as to the extent to which areas of endemicity correspond to Bretskyan entities, such as geobiomes, or to bioregions obtained by other methods. Before reviewing the methods used to detect endemic areas, it is essential to examine this issue. For smaller entities (e.g. holobionts), the correspondence is obviously poor, as the distribution ranges of species assemblages are rarely confined to a very small area or a single organism. In contrast, for larger areas (e.g. islands or continents), the correspondence is likely to increase, since significant dispersal barriers at larger scales often separate not only populations of the same taxon but entire species (Spiridonov & Eldredge, 2024). The similarity between bioregions derived from other bioregionalisation methods and endemic areas will largely depend on the (dis)similarity metric employed. Metrics based on presence–absence data (e.g. Jaccard, Sørensen) are more likely to capture patterns of endemicity, whereas those based on relative frequencies or species abundances (e.g. Morisita-Horn) lack such a mathematical predisposition.

Nonetheless, the correspondence between endemic areas and Bretskyan geobiomes is not perfect because the definition of endemic areas requires a rather strict congruence of species' distribution ranges, whereas the definition of Bretskyan entities relies on the compartmentalisation and integration of actual populations. Consequently, individuals of the same species may occur beyond the boundaries of a Bretskyan entity. In extreme cases, Bretskyan entities may consist entirely of populations whose species' ranges extend far beyond the entity's limits (e.g. in a lake ecosystem), resulting in little or no correspondence with endemic areas. However, if the compartmentalisation of populations persists over time, allopatric speciation due to vicariance should occur, meaning that Bretskyan entities—if strongly and persistently isolated by dispersal barriers—are likely to converge with, or at least resemble, endemic areas over time.

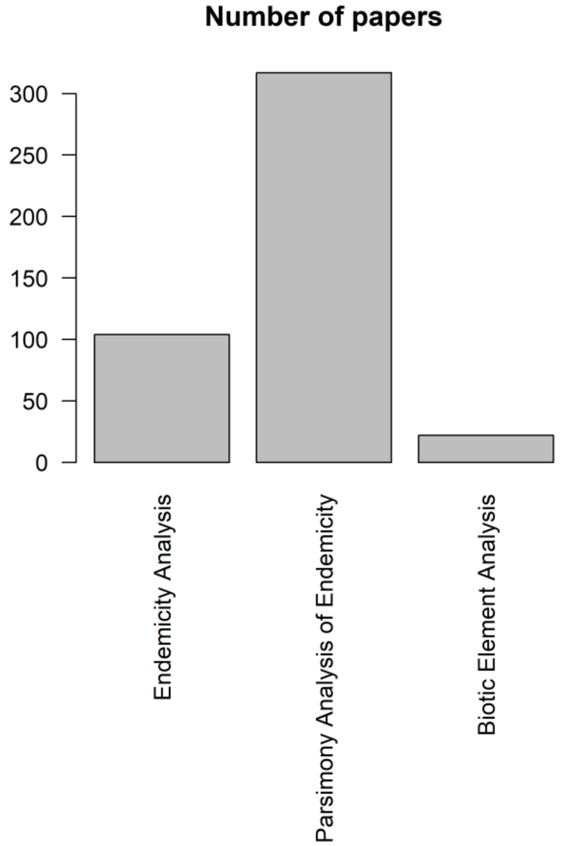


Figure 9. Number of Google Scholar search results (last checked on 8 April 2025) for the phrase '"X" "biogeography"'—where X is the method's name—restricted to publications from 2020 onwards. The sum of all papers here is higher than in aggregated result in Fig. 4 since some studies were comparative, applying more than one method to detect areas of endemism.

Given the real-world nature of the Bretskyan hierarchy and its material nesting, every life-inhabited point in space and time belongs to at least several Bretskyan entities at different hierarchical levels, each with varying degrees of compartmentalisation, integration, and consequent boundary fuzziness (Spiridonov & Eldredge, 2024). In other words, a map depicting the extents of Bretskyan entities would show no "empty spaces". Traditional approaches, such as cluster, network, and ordination analyses, can identify biotic clusters of localities which, when mapped, yield a spatially complete coverage. In contrast, maps of endemic areas typically exhibit many blank regions where there is little or no congruence in taxa distribution (though see Morrone (2014) and Brian R. Rosen (1988) for discussions suggesting that endemicity is relative and can be understood as a spatially scaling, hierarchical phenomenon). Nevertheless, the delineation of endemic areas still conveys important information that may be useful for detecting significantly compartmentalised—and thus more distinct—Bretskyan entities, providing a complementary perspective to other methods.

Endemic areas identified in recent biota may correspond to biodiversity hotpots, aiding in biotic preservation (Noroozi et al., 2018). On the other hand, endemic areas identified in the fossil record may be influenced by taphonomic factors; for example, Konservat Lagerstätten (sites of exceptional preservation) might appear as zones of high endemicity due to the presence of soft-bodied taxa or other organisms that are rarely preserved under more common taphonomic conditions.

Here three methods will be overviewed for endemic area identification: Parsimony Analysis of Endemicity, Endemicity Analysis, and Biotic Element Analysis. The most popular of these is Parsimony Analysis of Endemicity (Fig. 9).

Parsimony Analysis of Endemicity

Parsimony Analysis of Endemicity (PAE) is a biogeographic method designed to uncover hierarchical patterns of endemism, aiding in the inference of ecological and historical biogeographical connections between sample localities (Huang et al., 2010; Morrone & Escalante, 2002; Myers & Giller, 1988; B. R. Rosen, 1988; Rosen & Smith, 1988). It is based on the principle of parsimony analysis, which is traditionally employed to reveal phylogenetic relationships between taxa using their phenotypic traits.

In parsimony analysis, phylogenetic relationships are inferred by grouping taxa based on shared traits, aiming to construct the tree that requires the fewest evolutionary changes (e.g., trait gains or losses). Each possible tree is evaluated according to the number of changes needed, and the most parsimonious tree—the one with the least homoplasies—is considered the most preferable (Harper, 1999). This approach operates under the assumption of Occam's razor: that simpler explanations (fewer changes) are more likely to reflect true evolutionary pathways than complex ones. Parsimony is a useful methodological construct even though homoplasy is not rare in nature, and evolution itself is not parsimonious (Harper, 1999).

In Parsimony Analysis of Endemicity (PAE), the parsimony analysis algorithm is applied to differently structured data matrices: sample localities replace taxa in the columns, while contemporaneous taxa replace traits in the rows. The presence of a particular taxon in a locality is analogous to the presence of an advanced trait in traditional parsimony analysis, and taxa that appear exclusively in a group of localities are analogous to synapomorphies. These endemic taxa are instrumental in grouping areas based on their shared endemicity.

Figure 10. Cladograms of sample localities based on PAE analysis for extant reef coral and clypeasteroid echinoid genera. (a) Detailed coral data area cladogram, (b) Detailed echinoid area cladogram, (c-d) simplified consensus cladograms. Numbers following locality names in a-b indicate the count of genera shared with at least one other locality. Reproduced and modified with permission from B. R. Rosen (1988).

The outcome of this analysis is a hierarchical grouping of sample localities according to their shared endemic taxa (Fig. 10), revealing spatially-scaling hierarchical patterns of endemism (Morrone, 2014). Although such area cladograms can be employed to identify areas of endemicity and to infer historical, tectonic, and ecological influences on the spatial structuring of biota (Myers & Giller, 1988; B. R. Rosen, 1988; Rosen & Smith, 1988), there remains an ongoing debate regarding the value of the method (Huang et al., 2010; Morrone, 2014; Nihei, 2006; Peterson, 2008) and the extent to which its results accurately reflect historical biogeographical consequences of tectonic events (Morrone & Escalante, 2002; Myers & Giller, 1988; Nihei, 2006; B. R. Rosen, 1988).

Nevertheless, the prevailing view is that a dynamic interpretation—which examines changes in the PAE cladogram over time—is valuable for identifying historical biogeographic events (Morrone, 2014; Myers & Giller, 1988; Nihei, 2006). While PAE is recognised as a useful tool for revealing areas of endemicity, other methods, such as Endemicity Analysis (EA), may offer more robust results for this purpose (Huang et al., 2010; Morrone, 2014; Morrone & Escalante, 2002; Nihei, 2006).

Beyond the issues already mentioned, further criticism of PAE has been raised (e.g. Morrone, 2014; Nihei, 2006; Peterson, 2008), as is common with any method. However, with regard to its suitability for analysing spatiotemporal biotic structure, certain limitations merit closer attention. Consequently, an exhaustive overview of all limitations will not be provided; instead, the focus will be on those most pertinent to this thesis.

First, PAE's perspective is markedly different from the approaches previously discussed—a distinction that is both a strength and a weakness. While it may offer an independent and complementary viewpoint, it may also fail to produce results that are readily comparable with those generated by other methods.

Second, the area cladogram produced by PAE is based solely on the number of endemic taxa shared among the identified endemic areas. Although this measure might seem to offer a straightforward index of endemicity and similarity, it is not normalised in the manner of most ecological (dis)similarity measures (Legendre and Legendre, 2012a). Consequently, even if the number of shared taxa is displayed on the cladogram, the overall compositional (dis)similarities between endemic areas remain unclear. As a result, PAE outcomes are largely qualitative, with the relationships between endemic areas reflected only in the hierarchical topology of the cladogram.

Another issue is that the number of taxa not shared also influences the grouping of endemic areas. Although Morrone (2014) contends that this is acceptable—since shared absences could be interpreted as common extinction events—it is more likely that common absences arise from the fragmentary nature of the fossil record (Antell et al., 2024; Patzkowsky & Holland, 2012), which is affected by sampling and preservation biases. Moreover, assuming that absences reflect local extirpations implies that each taxon originally had a global distribution, an assumption that is ecologically and biogeographically untenable. Finally, most authors agree that absences are much less informative than presences, and that the most useful ecological (dis)similarity metrics are asymmetric, as they do not weight absences in the same way as presences (Legendre & Legendre, 2012a).

Furthermore, as with other methodological frameworks discussed earlier, the choice of geographical units in PAE is not trivial. Some authors advocate using the smallest possible units (e.g. Myers & Giller, 1988; B. R. Rosen, 1988), yet comparative studies indicate that it is preferable to use natural areas—such as predefined ecoregions or bioprovinces—rather than artificial small quadrats (Morrone & Escalante, 2002). Others prefer to use larger areas as units of analysis to achieve a more comprehensive understanding of the biogeographic situation (Huang et al., 2010). Finally, PAE does not ensure spatial contiguity of endemic areas that are grouped together in the area cladogram.

In summary, while PAE can be a useful tool for revealing areas of endemicity and their interrelationships, its suitability for elucidating patterns organised according to the principles of the Bretskyan hierarchy appears to be limited in several respects.

Endemicity Analysis

Endemicity Analysis (EA) is a method related to Parsimony Analysis of Endemicity (PAE), though it primarily focuses only on the identification of endemic areas. EA is often considered to be more robust in identifying areas of endemicity, allowing to detect a greater number of such areas (Escalante, 2015; Escalante et al., 2009; Morrone, 2014; Morrone & Escalante, 2002; Noroozi et al., 2018). However, based on the number of sympatric taxa in the identified regions, PAE tends to outperform EA (Escalante, 2015).

EA operates by optimising criteria of endemicity (Szumik et al., 2002). The study area is initially divided into grid cells, after which the method attempts to combine adjacent cells into larger areas, calculating their endemicity scores using a selected criterion (Fig. 11). There are four related endemicity criteria, each representing a progressive relaxation of the preceding one. The first criterion is the strictest, offering a theoretically 'pure' measure of endemicity, while the fourth is more realistic, capturing less distinct areas of endemism.

Taxa contribute to the endemicity score of an area under the following conditions:

- Criterion 1: A taxa's distribution perfectly aligns with the area, and all cells have an identical taxonomic composition.
- Criterion 2: As above, but taxa may also be present in adjacent cells outside the area.
- Criterion 3: The same as criterion 2, but the cells within the area do not need to have identical taxonomic composition.
- Criterion 4: Taxa contribute to the score even if they are not present in every cell of the area, as long as they are relatively evenly distributed across the area.

These criteria were later modified to support (Szumik & Goloboff, 2004):

- The identification of spatially non-contiguous endemic areas.
- Partial taxa contribution, based on the extent of their distribution beyond the area.
- The detection of spatially overlapping areas of endemism, where those areas are defined by disjoint sets of taxa (Szumik & Goloboff, 2004).

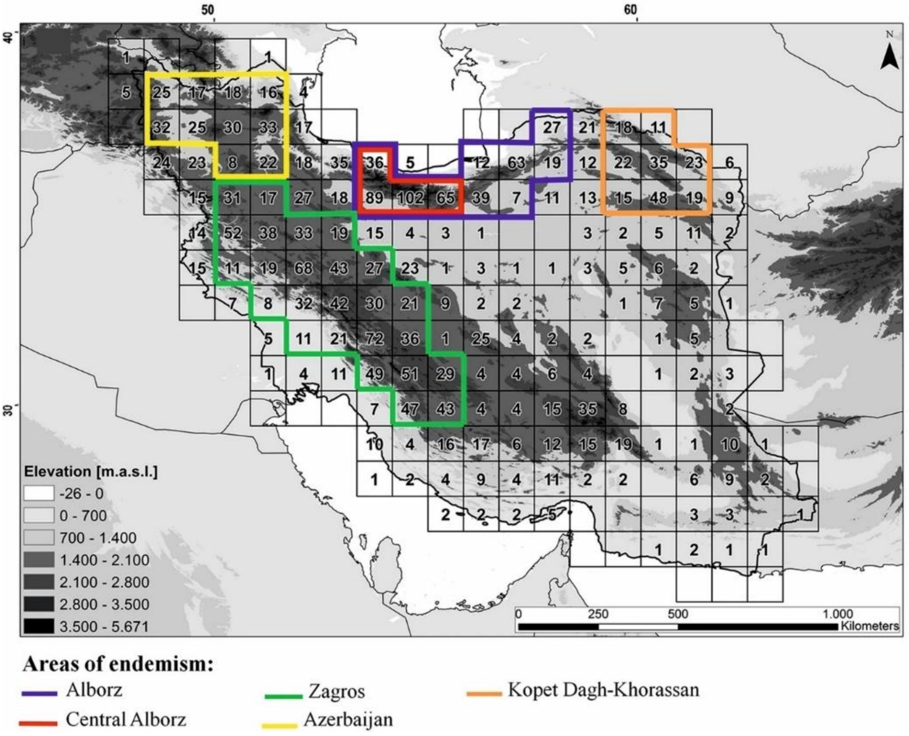


Figure 11. Endemic species richness of Asteraceae in Iran per grid cell, based solely on species occurring within the study area, with identified areas of

endemism outlined in colour. Reproduced and modified from Noroozi et al. (2018), licensed under CC BY 4.0 (http://creativecommons.org/licenses/by/4.0/).

The results obtained by applying different criteria are complementary in nature (Szumik et al., 2002). Compared to other methods, EA—like PAE—offers an independent perspective on biogeographical data, as it does not rely on the metrics commonly used in other methodological frameworks. However, this independence is also a weakness, as it reduces comparability with other methods. Moreover, both EA and PAE use presence/absence data; consequently, when working with abundance data, data generalisation is required, which results in the loss of potentially valuable information. In conclusion, because EA focuses solely on identifying areas of endemicity without revealing their hierarchical structure or relationships, it is ill-suited for understanding the hierarchical organisation of data structured according to the principles of the Bretskyan hierarchy.

Biotic Element Analysis

Biotic Element Analysis (BEA) offers a distinct approach to identifying endemic zones compared to other methods (Casagranda et al., 2012; Hausdorf & Hennig, 2003). Initially, it seeks to identify groups of taxa with similar distribution ranges—termed biotic elements—and subsequently projects these taxa clusters into geographical space, localizing endemic areas (Fig. 12). To identify biotic elements, BEA uses model-based Gaussian clustering (MBGC) applied to the results of non-metric multidimensional scaling (MDS) (Hausdorf & Hennig, 2003). At first glance, this approach may appear similar to conventional ordination-based clustering. However, it differs in several respects, most notably in its reliance on an entirely different (dis)similarity matrix. Whereas traditional approaches are based on matrices of taxonomic distances between locations, BEA employs a matrix that reflects range differences between taxa.

To obtain this matrix, occurrence data must first be generalised to derive the distribution ranges for each taxon. Then, using cell data that indicate the presence or absence of taxa, pairwise Kulczynski distances between taxa are calculated (Hausdorf & Hennig, 2003). The Kulczynski distance is defined as one minus the average ratio of the common area shared by two taxa to the total extent of their distribution ranges (i.e. $1 - ½(C/A + C/B)$, where C is the number of cells in which both taxa are present, A is the number of cells in which taxon A is present, and B is the number of cells in which taxon B is present). This Kulczynski distance matrix is subsequently subjected to non-metric multidimensional scaling and then used as input for model-based Gaussian clustering (MBGC). This process yields clusters of similarly distributed taxa. The strengths of MBGC lie in its ability to determine the number of significant clusters and to identify which taxa cannot be assigned to any cluster (e.g. cosmopolitan or uniquely distributed taxa) (Casagranda et al., 2012; Hausdorf & Hennig, 2003).

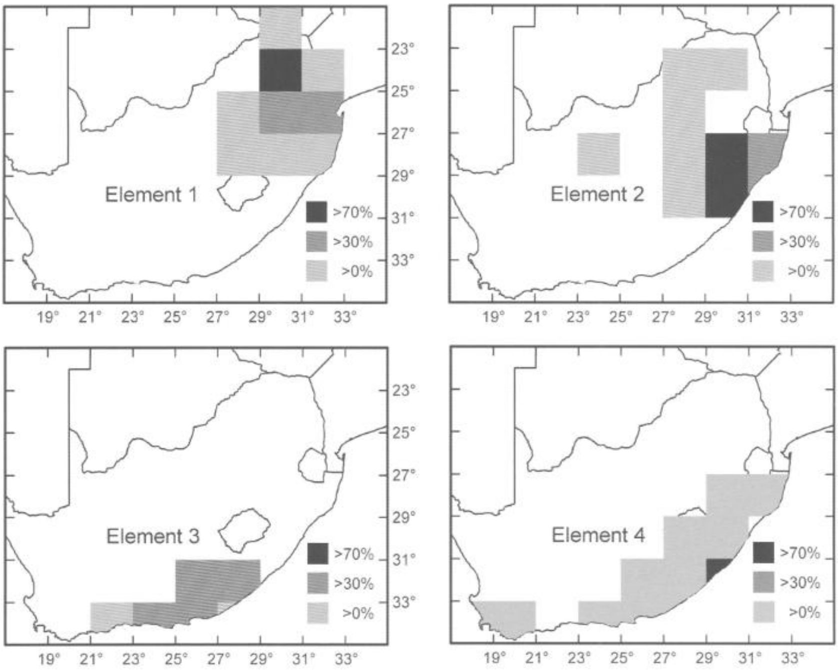


Figure 12. Distribution maps of four biotic elements based on the mapped ranges of South African Scobius species on a 2° grid (with some Namibian grid squares omitted). Shading indicates areas where more than 70%, more than 30%, and more than 0% of an element's species are present. Reproduced with permission from Hausdorf and Hennig (2003).

Additionally, BEA employs a stochastic Monte Carlo simulation method to test for the clustering of distribution areas, accounting for the distribution of range sizes, variation in the number of taxa per cell, and the autocorrelation of occurrences.

The resulting biotic elements can be projected onto geographical space with varying levels of completeness (Hausdorf & Hennig, 2003). For example, a complete representation of a biotic element would include all cells that contain at least one taxon belonging to that element, whereas a more restricted representation—more closely aligned with the concept of an endemic area—

would consist only of those cells in which a substantial proportion (e.g. 70%) of the taxa belong to that biotic element.

Although theoretically BEA appears to be a sound method, formal comparisons with PAE and EA have highlighted several issues regarding its ability to delimit endemic areas (Casagranda et al., 2012). Most notably, it can produce counterintuitive results whereby allopatric taxa are assigned to the same biotic element, or fully sympatric taxa are assigned to different elements (Casagranda et al., 2012). Consequently, EA remains the most robust method for delimiting endemic areas. With respect to what BEA can contribute to our understanding of hierarchical Bretskyan structuring, its value is uncertain. Given that this method is not hierarchical, and that the biotic elements it identifies often overlap in space or are even spatially discontinuous (see biotic elements obtained in Hausdorf & Hennig (2003)), interpreting BEA results within the context of Bretskyan hierarchy theory may prove challenging.

2.1.2.Bioregion Analysis Methods

Once bioregions have been delineated, a range of methods can be employed to investigate their characteristics. In this section, brief review of these methods and the associated traits they assess will be provided, though the emphasis of this thesis remains on the delineation of bioregions.

Clarke (1993) proposed two widely used techniques: Analysis of Similarities (ANOSIM) and Similarity Percentage Breakdown (SIMPER). ANOSIM functions as a non-parametric analogue of ANOVA, specifically adapted for species composition data. It tests the null hypothesis that community composition does not differ significantly between bioregions.

The ANOSIM procedure is relatively straightforward: a similarity matrix is calculated for all samples, and all similarity values are ranked. The average similarity within bioregions (RW and between bioregions (RB) is then computed. These values are used to calculate the test statistic $R = (RB – RW) / (M / 2)$, where M is the number of pairwise comparisons. To assess statistical significance, a permutation-based approach is employed: species labels are randomly shuffled, and the R statistic is recalculated multiple times (e.g. 1,000 permutations). The p-value of the observed R is then derived from this null distribution. ANOSIM can thus serve as a useful tool for validating delineated bioregions, particularly when the bioregionalisation method applied does not include built-in validation tools.

SIMPER, by contrast, identifies the degree to which each species contributes to differences between bioregions. In this method, Bray–Curtis dissimilarity between two bioregions j and k is decomposed into the sum of species-specific contributions to overall dissimilarity, *δjk (i)*:

$$\delta_{jk} = \sum_{i=1}^{p} \delta_{jk}(i)$$

Eq. 4

In eq. 4 and 5, i denotes a species and p is the total number of species. The contribution of species i to the Bray–Curtis dissimilarity between bioregions j and k is expressed as a percentage:

$$\delta_{jk}(i) = 100 \cdot \frac{\left| y_{ij} - y_{ik} \right|}{\sum_{i=1}^{p} \left(y_{ik} + y_{ik} \right)}$$

Eq. 5

To obtain the average contribution of species *i* to the dissimilarity between two bioregions, *δjk (i)* is calculated for all sample pairs between those bioregions and then averaged. The standard deviation of these contributions reflects the consistency of the species' influence across samples. For this purpose, the ratio between the average contribution and its standard deviation can be particularly informative (Clarke, 1993).

An obvious limitation of the SIMPER approach is that it relies on the Bray–Curtis dissimilarity metric, which is restricted to abundance data. Moreover, it identifies species contributions to a specific pairwise partition (i.e., between two bioregions) rather than to the overall grouping structure. However, the SIMPER approach could be extended to accommodate other dissimilarity metrics, and species contributions to the overall grouping could be summarised using the mean and standard deviation of their average contributions across all bioregional partitions.

Another valuable method for characterising the composition of delineated bioregions is the Indicator Species Analysis (IndVal) approach (Dufrene & Legendre, 1997). Although originally developed for use with abundance data, the IndVal index can be readily adapted for presence–absence data. The index is calculated as the product of two components: specificity (*Aij*) and fidelity (*Bij*).

In the case of occurrence data, specificity would be defined as:

$$A_{ij} = \frac{N_{occ_{ij}}}{N_{occ_{i\cdot}}}$$

Eq. 6

In eq. 6 and 7, $N_{occ_{ij}}$ is the number of occurrences of species *i* in bioregion *j*, and $N_{occ_{i\cdot}}$ is the total number of occurrences of species *i* across all bioregions. Similarly, fidelity, in case of occurrence data cases, would be defined as:

$$B_{ij} = \frac{N_{occ_{ij}}}{N_{sites_j}}$$

Eq. 7

In eq. 7, N_{sites_j} is the total number of sites in bioregion *j*. The IndVal is then expressed in percentage form:

$$IndVal_{ij} = A_{ij} \times B_{ij} \times 100$$

Eq. 8

The maximum IndVal value across all bioregions for a given species *i* indicates the bioregion that is most characteristic of that species' distribution (Dufrene & Legendre, 1997). Conversely, the maximum IndVal across all species for a given bioregion can be used to identify the species most indicative of that bioregion.

If palaeoenvironmental variables are available, bioregions and taxa can be characterised and compared in terms of their environmental context. Hutchinson (1957) introduced the concept of the ecological niche as a hypervolume in n-dimensional environmental space within which a species can persist (Brown, 1995). Building on this conceptual framework, a variety of indices have been developed to quantify niche characteristics such as breadth and overlap (Blonder et al., 2014; Broennimann et al., 2012; Colwell & Futuyma, 1971; Levins, 1968; Slatyer et al., 2013; Warren et al., 2008). These indices can be adapted to define and compare the environmental conditions of bioregions. Furthermore, such metrics can be used to classify taxa as specialists or generalists (Levins, 1968), and by extension, bioregions can be characterised according to their ratio of specialists to generalists.

The boundaries that separate identified bioregions also represent a valuable by-product of bioregionalisation analysis. Their characteristics—such as shape, scale, sharpness, width, and correspondence with environmental boundaries—can be explored using boundary analysis techniques (see Boundary Analysis Methods section). Investigating these traits, alongside those of the bioregions themselves, can yield a rich and nuanced understanding of biotic organisation. For example, the ANOSIM method can be employed to validate the identified bioregional structure, while SIMPER and IndVal analyses can reveal which taxa contribute most significantly to the observed biotic subdivision patterns. Considering the physiology and ecological niche requirements of these taxa may generate hypotheses regarding key environmental drivers. Where independent palaeoenvironmental data are available, such hypotheses can be tested by characterising and comparing the environmental conditions associated with different bioregions. In spatiotemporal study designs (e.g. Button et al., 2017; Halliday et al., 2020), it may also be possible to examine how the traits of bioregions and their boundaries evolve through time.

2.1.3. Summary

Bioregionalization methods encompasses a wide spectrum of methodological approaches, each with its own strengths, assumptions, and limitations. Traditional cluster analysis, while foundational, often fails to ensure spatial contiguity and does not output boundaries. Spatially constrained variants attempt to mitigate some of these issues but still inherit other limitations. Ordination methods provide a powerful exploratory lens to uncover gradients and complex variation, yet they too lack explicit hierarchical or spatial contiguous structuring and boundaries. Network analysis offers an increasingly popular and flexible alternative that can accommodate complex relationships and integrate diverse data types, but it likewise struggles with defining spatial boundaries, preserving ecological distance interpretations, and ensuring spatial contiguity of bioregions. Moreover, all these three method groups rely on input distance matrices, which often have biased entries due to sample size issues discussed, and are not suited for the analysis of data dominated by geographical singletons (localities with singular occurrence).

Complementing these general approaches are methods for detecting areas of endemism, such as Parsimony Analysis of Endemicity, Endemicity Analysis, and Biotic Element Analysis. These methods, while less popular, offer valuable insights into taxonomic uniqueness and evolutionary compartmentalisation, yet their applicability to patch-based Bretskyan-like hierarchical frameworks remains limited due to their reliance on strict congruence of taxa ranges. Most geobiomes are unlikely to correspond well to areas of endemism.

Ultimately, no single method fully captures the multifaceted nature of Bretskyan hierarchical structuring. However, by understanding the capacities and shortcomings of each approach—and using them in complementary ways where possible—it is possible to gain a richer, more nuanced understanding of how biotic communities are structured across space and time. Future methodological developments should aim to integrate the strengths of existing approaches while addressing their shortcomings, particularly in spatial boundary definition, hierarchical representation, and ecological interpretability. As consequence, the methodological approach proposed in this thesis –HespDiv–will try to address these issues.

2.2. Boundary Methods

Biotic boundaries are regions where biotic turnover is more rapid than in surrounding areas. In essence, bioregions and the boundaries that separate them go "hand-in-hand" as they are mutually defining: the presence of boundaries reveals distinct bioregions, and the existence of bioregions implies the presence of intervening boundaries.

The methods previously described for bioregionalisation are primarily designed to identify spatial clusters of biotic data—that is, areas where the biota is relatively homogeneous or, in other words, where significant spatial biotic turnover is absent. Consequently, the results of these analyses implicitly delineate biotic boundaries as the transition zones between spatial clusters. One approach to identifying biotic boundaries, therefore, is to first delineate bioregions using the methods outlined in the preceding section. However, boundaries obtained in this manner are always closed (forming continuous loops), whereas in reality, biotic turnover can vary considerably across space, with open boundaries being far more common in nature (Kent et al., 2006). As such, mainstream bioregionalisation methods that confine outputs to closed boundaries may face challenges in accurately capturing the spatial discontinuities of "real" biotic boundaries. Nonetheless, they remain practical for generating well-defined spatial units that can be used in subsequent analyses. Conversely, the issue with open boundaries is that they are inherently local in character, making it difficult to extrapolate clearly defined bioregions from them. This likely explains why methods designed to detect bioregions are considerably more popular than those focused on boundary detection (cf. Figs. 4, 13). Still, the prevalence of open boundaries in natural systems underscores the importance of boundary detection methods, and thus they are included in this overview of methodologies for investigating the spatiotemporal organisation of biota.

In the first part of this section, two independent approaches for identifying open biotic boundaries will be reviewed: the split moving-window (SMW) method and wombling. Although both are relatively underemployed in contemporary biogeographical research, wombling has seen slightly broader application (Fig. 13).

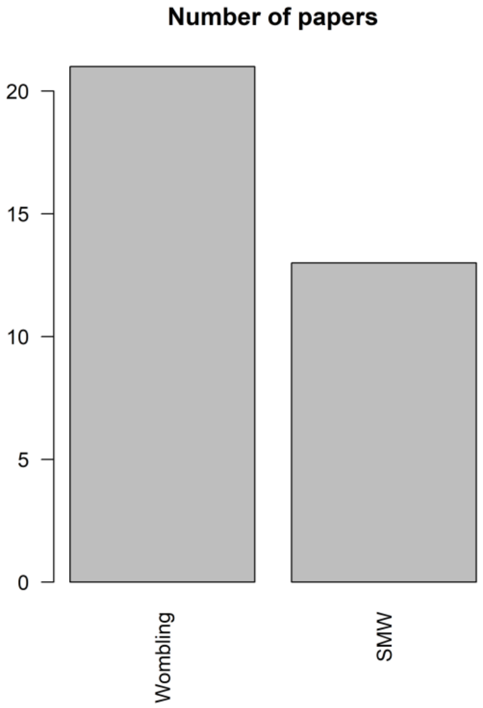


Figure 13. Number of Google Scholar search results (last checked on 8 April 2025) for the phrase '"X" "biogeography"'—where X is the method's name—restricted to publications from 2020 onwards. Since split moving-window (SMW) is sometimes referred to as moving split-window (MWS), the searching phrase used was: "biogeography" ("Split Moving Window" OR "Moving Split Window").

Once boundaries or bioregions have been established—an outcome common and widely accepted in many studies—one is still facing a bewildering array of questions. Why do these boundaries exist? Which environmental factors, and in what ways, contribute to their formation? How does biotic turnover vary along a given boundary and temporally? Is the turnover confined to a narrow strip, resulting in an ecotone, or is it more diffuse, with significant differences emerging only over larger distances perpendicular to the boundary, thereby producing an ecocline? There is also the question of scale: How would the boundaries appear at different scales? Moreover, which taxonomic groups are most strongly differentiated by these boundaries, and which show little response? Are there groups that support different sets of boundaries? We can condense and generalise these questions into a single, more complex query: What properties do these boundaries have, how do they change across space and time, how do they depend on scale and taxonomic group, and how do they correlate with environmental surfaces? The point here is that the mere identification of boundaries unearths a myriad of questions that demand further exploration. Thus, in the second part of this section, approaches designed to address these queries will be discussed, elucidating the underlying drivers and nature of biotic turnover along boundaries.

2.2.1 Boundary Detection methods

With regard to dimensionality, boundaries can be classified as 0D, 1D, and 2D. 0D boundaries are simply points that partition ordered data (e.g. taxonomic variation along a spatial transect); thus, they have zero dimensions. In contrast, 1D and 2D boundaries correspond to spatial and spatiotemporal boundaries, respectively. Various techniques exist for identifying 0D boundaries—such as constrained cluster analysis, global zonation, comparison of successive adjacent pairs of points, ordination scores along a transect, and wavelet analysis—with the split moving-window method being among the most versatile (Cornelius & Reynolds, 1991; László et al., 2014). Methods for delineating 1D boundaries are generally referred to as wombling, and spatiotemporal wombling represents an extension for detecting 2D boundaries. In this section, the split moving-window and wombling methods will be presented, along with their various extensions.

Split Moving-Window

The origins of the split moving-window (SMW) methodology are linked to early attempts to measure ecological change along topographical gradients (Kent et al., 2006). Whittaker was likely the first to apply this approach in an effort to track vegetation changes along topological gradients (e.g. altitude, moisture, etc.) in the Siskiyou Mountains, USA (Whittaker, 1960). A key feature of the method is that it enables the identification of 0D boundaries in

1D spatial data—that is, points that partition a spatial transect into contiguous intervals.

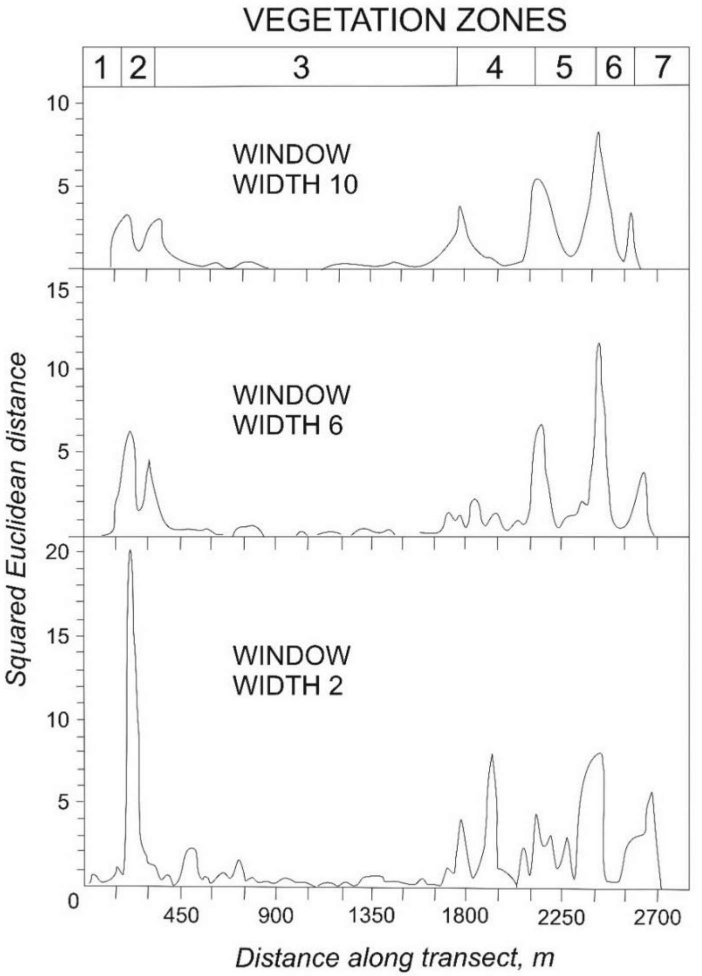


Figure 14. Example of SMW output, and how it depends on the scale of analysis (window width). The high peak obtained with a narrow window of width 2, represents an ecotone, whereas peaks visible using broader windows correspond to more fuzzy boundaries or ecoclines. Reproduced and modified with permission from Ludwig and Cornelius (1987).

The principle of SMW is straightforward (Webster, 1978):

1) Select a spatial transect along which boundaries are to be identified.
2) Then move a window of predefined dimensions along the transect. The window is split in the middle into two halves, with the split oriented perpendicular to the transect.

3) The two halves of the window are used to sample data on either side of the split as the window moves, and the sampled datasets are compared using a selected difference function to obtain a difference value for each position along the transect.
4) This process results in a SMW profile.
5) Finally, boundaries are drawn at significant peaks in the difference values (e.g. Fig. 14).

The method involves several parameters, the selection of which is not trivial. The dimensions of the split window, particularly its width, determine the scale of analysis; narrow windows can be used to identify ecotones, whereas broader windows can detect ecoclines (see Fig. 14). The window's height controls how close observations must be to the transect to be included in the analysis. The step size—that is, the distance by which the split window is moved each time—essentially governs the granularity of the analysis. Finally, the difference function determines the final output values for each position along the transect (usually, a quadratic Euclidean distance is employed; (László et al., 2014). Perhaps the most important input is the transect itself, including its length and its spatial positioning relative to the observations.

Traditional applications of the SMW approach do not provide formal estimates of boundary significance; instead, boundaries are identified subjectively by drawing them at the peaks of the difference values. This represents a serious problem, as random noise can also generate discontinuities that appear significant (Cornelius & Reynolds, 1991). An overview of SMW studies reported that 45% of the studies did not use any significance testing, while 7.5% applied an arbitrary significance rule (László et al., 2014).

Distinct approaches exist for identifying both scale-dependent and scale-free significant boundaries. Cornelius and Reynolds (1991) introduced a Monte Carlo-based method in which observation positions along the transect are randomised—while retaining their correlation structure—to generate multiple SMW profiles. These profiles are then used to produce confidence intervals for the difference values at each transect position. Scale-specific significant boundaries are defined as those positions where the observed peak in non-randomised data exceeds the mean plus 2σ (i.e. the 95% confidence interval) since the Monte Carlo-derived difference values follow a standard normal distribution.

For scale-free boundary significance estimation, a pooled SMW difference profile is generated by running SMW at various scales (Cornelius & Reynolds, 1991). The resulting profiles are normalised using the Monte Carlo mean and standard deviation estimates, yielding z-value profiles that are then averaged to form a pooled profile. This pooled profile is recursively partitioned at its highest peaks into hierarchically organised segments (Cornelius & Reynolds, 1991). The obvious drawback of this procedure is that it assumes the existence of scale-free boundaries; in reality, a given boundary may be significant over a range of scales but not uniformly so. Comparisons of SMW profiles across different scales reveal autocorrelation based on scale (e.g. 8), meaning that significance of boundary might taper off with changing scale. Thus, peaks in the pooled profile may still correspond to boundaries that are only significant at certain scales. Focusing solely on boundaries that are consistent across all scales results in a loss of nuance regarding how the significance of discontinuities varies with scale. An extensive review of SMW studies similarly recommends against averaging SMW profiles across scales (László et al., 2014).

A second limitation of conventional significance testing is that significance estimation is adversely affected by decreasing transect length and an increasing number of boundaries (Körmöczi, 2005). Among various methods for randomising data to construct a null model for SMW boundaries, the approach that randomly shifts species data along the transect appears to perform best, whereas complete randomisation performs most poorly (László et al., 2014).

To summarise, SMW represents a powerful yet simple spatial data exploration technique, capable of locating 0D boundaries in 1D transects. However, its inherent dimensionality is a serious drawback. There are SMW designs that can yield boundaries with more dimensions; for example, analysing many parallel SMW profiles concurrently can lead to 1D boundaries (Kröger et al., 2009), and incorporating a temporal perspective into these analyses could yield spatiotemporal surfaces or 2D boundaries. A second notable challenge with SMW is the large number of parameters that influence the results. Although the selection of window dimensions, the difference function, and spatial transect parameters may introduce some unnecessary subjectivity into the analysis, these choices also provide opportunities to explore a wide range of queries that may not be possible with other approaches (see the section boundary properties). Thus, although SMW approaches represent a rather simplistic paradigm, they will likely remain relevant and may even see increased adoption, given their potential to address various research questions by leveraging the multitude of parameters and the extensive data used to support a single 0D boundary.

Wombling

Wombling is the analysis of the spatial rate of change of variables and is named after its developer, Womble (1951). The approach has applications in a wide array of fields (image processing, landscape topography, ecology, medicine, linguistics, particle physics), and is also known as edge detection, boundary analysis or barrier analysis (Barbujani et al., 1989; Fitzpatrick et al., 2010; Liang et al., 2009; Lu et al., 2007; Matchev et al., 2020). Initially, the adoption of this method was inhibited by the lack of large, regular spatial datasets and computing power; only with advances in computer technology and the advent of big data did wombling begin to be applied in practice (Barbujani et al., 1989). Since then, multiple extensions of wombling have been developed to support a wider array of datasets and to estimate the significance of identified boundaries (Kent et al., 2006).

The principal idea behind wombling is relatively straightforward: one approximates the systemic function—the spatial surface defined by variable values at given points—by interpolation. Subsequently, one calculates the partial derivatives of the systemic function to determine the direction and magnitude of the steepest gradient at various locations (Kent et al., 2006). When multiple variables are used for boundary detection, both boundary strength and direction are averaged across all variables. Next, one locates adjacent points that exhibit outstanding average turnover rates and connects them with lines to represent boundaries; alternatively, "rods" can be drawn perpendicular to the boundary, oriented according to the average direction of the maximum turnover rates across all variables (Barbujani et al., 1989).

The original wombling approach was lattice wombling (Barbujani et al., 1989). As the name implies, this method requires input data points arranged in a regular spatial lattice or grid. The interpolation function employed is bilinear, interpolating variable values within each lattice square defined by four corner points. Partial derivatives of this interpolation function with respect to x and y coordinates are calculated for the central point of each lattice square; these derivatives represent the average spatial turnover rates in orthogonal directions. Combining these derivatives as vectors yields the direction and magnitude of the maximum rate of change.

If multiple variables are analysed simultaneously, their respective directions and magnitudes of turnover must be combined to obtain an average. Average magnitude can be computed as the ordinary mean (assuming comparable variable scales; if not, prior scaling should be performed). To calculate the mean direction, vectors representing maximum turnover rates are first scaled to unit length, after which their angles are doubled, and de-doubled (to correct for opposite directions representing the same orientation). These vectors are then combined to yield a resultant vector. The resultant vector's direction indicates the average direction of maximum turnover, while its length represents orientation variability (shorter lengths indicate more variable orientations). Angle doubling (and subsequent halving of the resulting angle) is necessary because boundary orientation, rather than boundary direction, is of interest; otherwise, vectors facing opposite directions would incorrectly cancel each other out. This angle-doubling method is thoroughly described in Davis (2002).

A detailed description, complete with mathematical formulas and visual examples of this wombling approach, can be found in Barbujani et al. (1989).

The primary limitation of lattice wombling is its requirement that data be arranged on a regular spatial grid, a condition rarely satisfied by palaeontological data (Antell et al., 2024). Moreover, the ability to apply bilinear interpolation and calculate partial derivatives relies on data being continuous, and the fractal and multifractal structure which implies roughness is expected (Spiridonov et al., 2016). Thus, considering that fossil occurrences—typically presence–absence data—represent the core datasets for exploring the spatiotemporal structure of the biotic world, lattice wombling in its original form has further limitations.

Fortunately, extensions of wombling methodology have since been developed, removing the requirement for data to be regularly spaced and enabling analysis of categorical data (Kent et al., 2006). For instance, triangular wombling (Fortin, 1994). approximates the variable surface using triangular planes, with data points at triangle vertices. The triangles are derived from Delaunay triangulation (see subsection on General Spatially Constrained Hierarchical Clustering for a detailed explanation). Partial derivatives are then calculated at each triangle’s centroid to estimate spatial rates of change in two orthogonal directions. These rates are combined into vectors, indicating the direction and magnitude of the maximum turnover.

Categorical wombling, on the other hand, quantifies boundary strength by calculating the number or proportion of category changes occurring along edges defined by Delaunay triangles (Oden et al., 1993). This approach specifically accommodates categorical data, making it directly applicable to palaeontological fossil occurrence datasets.

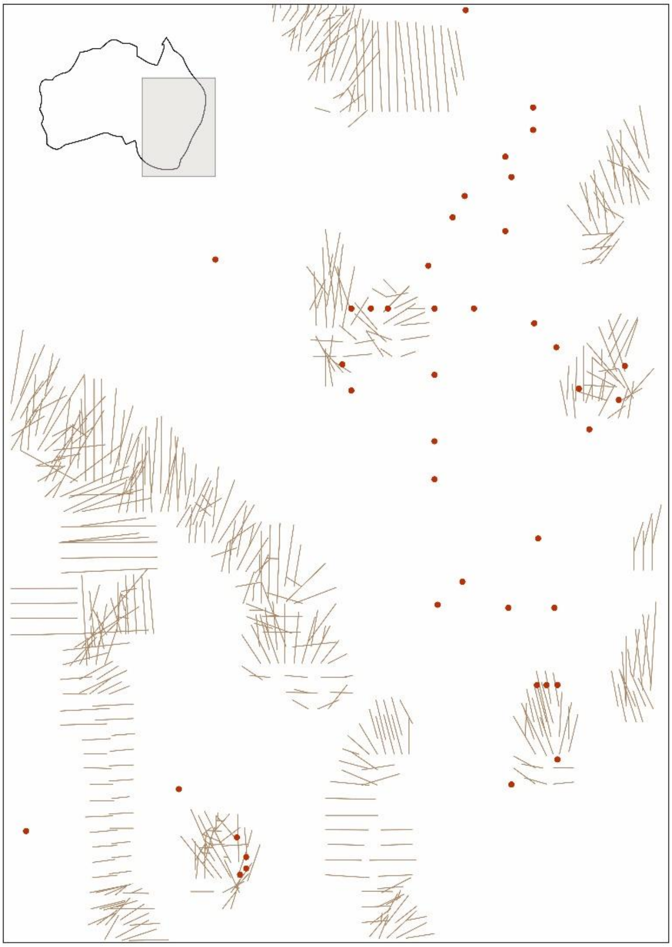


Figure 15. Boundaries produced by lattice wombling, based on the average orientation and magnitude of maximum rates of change in the frequencies of nine alleles in Australian *Drosophila buzzatii.* Boundaries are oriented perpendicular to the displayed rods, with rod length indicating boundary strength. Here, rods representing boundaries in the highest decile and 'bridge' boundaries in the second-highest decile of average turnover rates are shown. Dots represent locations of the studied *Drosophila* populations. The SYMAP interpolation algorithm was employed to create the regular grids required for lattice wombling. Note that identified boundaries are concentrated around the peripheries of the central distribution of locations, and several areas exhibit increased spatial heterogeneity in allelic frequencies. Furthermore, two larger bioregions could be inferred from these boundaries: one wedge-shaped region in the southwest and another located to its northeast. Rectangle at the top represent the study area location within Australia. Reproduced and modified with permission from Barbujani, et al. (1989).

The output of wombling is typically presented as a map depicting identified boundaries (e.g. Fig 15). Usually, only boundaries representing the strongest quantile of turnover rates (e.g. the 10th decile) are visualised, while weaker boundaries remain hidden. To enhance spatial continuity, 'bridge' boundaries may be included. These bridge boundaries, positioned between two stronger boundary segments, act as connectors and thus have slightly lower strength requirements (e.g. the 8th–9th deciles) (Barbujani et al., 1989).

The classical applications of wombling, similar to split moving-window (SMW) analysis, originally lacked methods to assess the significance of detected boundaries; however, this functionality was later introduced. Gleyze et al. (2001) proposed a test statistic, S, defined as the mean length of identified boundaries. Under the null hypothesis, boundaries are randomly distributed, and the expectation is that boundary lengths under randomness would be shorter compared to genuinely structured zones exhibiting rapid turnover. Their significance test relied on generating empirical distributions of boundary lengths through Monte Carlo simulations, using either a nudge effect or predefined variograms to simulate spatial data.

However, their original test performed poorly when boundaries were weakly structured, as gradients around local anomalies often overshadowed gradients along genuine boundaries, resulting in numerous short boundary segments—some corresponding to local anomalies and others being fragments of actual boundaries. A modification of wombling—achieved by allowing a greater number of 'bridge' boundaries and preventing rapid directional changes (thus avoiding circular boundaries around local anomalies)—significantly improved the performance of the test. The modified wombling procedure with boundary significance estimation was tested using metal concentration data (cobalt, chromium, nickel) from the Swiss Jura region, producing significant boundaries that closely matched major geological formation limits (Fig. 16). Therefore, this enhanced approach represents a substantial advancement in wombling methodology, constituting an important milestone in the development and practical application of this technique.

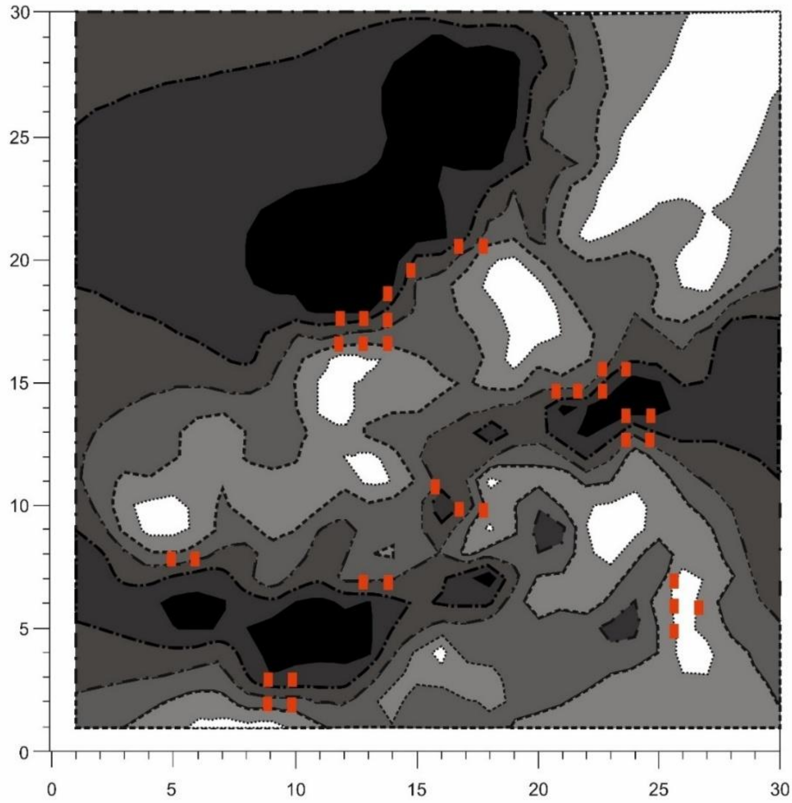


Figure 16. Map of the Swiss Jura region showing wombling boundaries (red rectangles) detected in cobalt concentrations. Map covers 30x30 grid over 14.5 km^2 geographic region. The boundaries were tested for significance using a Monte Carlo approach, employing the mean boundary length as a test statistic. Boundaries are superimposed on a kriging interpolation map. Reproduced and modified with permission from Gleyze et al. (2001).

Later developments in wombling introduced Bayesian approaches capable of producing posterior distributions of boundaries in space, expanded methodologies to accommodate areal input data (polygons instead of points), and extended wombling into the spatial point-process framework, where locations, instead of being fixed, are treated as random realisations of an underlying spatial process (Carlin & Ma, 2007; Fitzpatrick et al., 2010; Gelfand & Banerjee, 2015; Liang et al., 2009; Lu & Carlin, 2005; Lu et al., 2007; Matchev et al., 2020). These methodological advances were supported by the development of dedicated software tools such as the WOMBSOFT R package (Crida & S., 2007). Thus, these improvements broadened the applicability of wombling by supporting diverse input data, providing software implementations, and introducing additional statistical approaches to evaluate the significance of detected boundaries and their uncertainty.

A subsequent major milestone was the expansion of wombling methodology into the spatiotemporal domain, enabling the detection of spatiotemporal boundary surfaces. Recent publications indicate that this advancement has already been achieved (Halder, 2020; Halder et al., 2024). Another significant recent development is the extension of nonparametric approaches to detect boundaries in functional data—where observations themselves are functions or curves evolving over time or another continuous dimension (Barratt & Aston, 2025).

Therefore, over the past few decades, essentially since the advent of modern personal computers, wombling has undergone substantial evolution, progressing from early empirical implementations to sophisticated methodologies capable of detecting spatiotemporal boundary surfaces and discontinuities in functional data.

Compared to methodological developments in bioregionalisation, wombling appears more advanced in certain respects, particularly due to its successful extension into the spatiotemporal domain and its capacity to accommodate functional data. However, this does not imply that wombling should be preferred for bioregionalisation purposes. A key limitation of wombling is that the boundaries it produces represent only local-scale biotic turnover. The spatial scale at which this turnover is assessed is inherently determined by the level of spatial aggregation in the input data. For instance, if data points represent regional-level information, the resulting wombling boundaries may indeed reflect regional turnover. Nonetheless, for bioregionalisation tasks—particularly when the objective is to generate closed boundaries delineating spatially contiguous bioregions, or to produce hierarchical subdivisions of the study area—wombling is not an appropriate approach. Specifically, it is ill-suited to the identification of geobiomes as defined within the framework of Bretskyan hierarchy theory.

That said, once geobiomes have been delineated, wombling may offer valuable complementary insights. It could be employed to identify which geobiome boundaries align with zones of rapid local biotic turnover, and to determine whether similar turnover zones occur within individual geobiomes.

2.2.2. Boundary Analysis methods

Once natural boundaries in the underlying fossil occurrence or abundance data have been established, numerous questions arise regarding the characteristics of these boundaries. Fortunately, a variety of methods have been developed to explore such features. The available methodological toolkit enables the assessment of several key aspects of boundaries, including their statistical significance (if not already evaluated), zone of influence or width, sharpness or strength, geometric properties, scale-dependence, and coincidence with other boundaries.

Harper and Macdonald (2001) proposed a critical values approach to estimate the distance of edge influence (DEI) for variables of interest—an approach that can be readily extended to estimate boundary width. They applied this method to predefined natural lakeshore edges in order to examine their influence on boreal forests, focusing on variables such as species composition, canopy cover, tree and sapling density, vegetation cover, and plant height. Although their study was based on pre-existing boundaries, the methodology is equally applicable to boundaries identified through techniques such as split moving-window (SMW), wombling, or even some bioregionalisation methods.

The principle of the approach is straightforward (Harper & Macdonald, 2001): first, transects are positioned perpendicular to the boundary whose influence is to be evaluated. At various distances from the boundary, mean values of the variables of interest are calculated. A reference dataset—typically from transects placed in control areas assumed to be free from boundary effects (e.g. riparian or interior forest zones in their study)—is then used to build an empirical distribution of mean values via randomisation, usually involving a large number of iterations (e.g. 5,000). The quantiles of observed values along the focal transects are then assessed: edge influence is inferred at points where values fall below the 2.5th percentile or above the 97.5th percentile of the empirical distribution.

This approach offers several advantages. It is robust to violations of normality and is unaffected by spatial autocorrelation, as the spatial structure of the data is preserved during the randomisation process (Harper & Macdonald, 2001). However, the original implementation considered DEI only in one direction away from the boundary. This can be readily extended by analysing both directions perpendicular to the boundary. Summing the DEI values from each side would provide an estimate of the total boundary width. Moreover, the joint profile of variable means across the boundary can yield further insights—for instance, whether the variable distribution is symmetrical around the boundary, skewed to one side, or displays a more complex structure.

For similar purposes, the split moving-window (SMW) approach can also be applied (e.g. Harper & Macdonald, 2001). SMW transects can be positioned at regular intervals along contiguous boundaries identified by wombling or bioregionalisation methods. These transects should be centred on the boundary and oriented perpendicularly to it. The SMW profiles derived from such transects can provide insights into the width and strength of the boundary. By varying the window width, it becomes possible to identify the range of scales over which the boundary remains detectable.

To fully exploit the multiscale capabilities of the SMW method, a two-dimensional plot can be constructed in which the ordinate represents scale (i.e. window width), the abscissa represents position along the boundary, and the SMW difference values at each point are visualised through colour-coding—similar to power spectrum plots used in wavelet analysis. Although some studies have explored SMW profiles across multiple scales (László et al., 2014), this form of visualisation does not appear to have been previously implemented.

Wavelet analysis can also be employed to detect 0D boundaries in spatial transects in a manner similar to SMW. Haar wavelets are particularly well suited for this task due to their step-like structure, which is ideal for identifying abrupt transitions (Bradshaw & Spies, 1992). In addition, wavelet variance can be calculated at each scale, providing information about the scales at which turnover variability is most pronounced (Bradshaw & Spies, 1992).

Biogeographical studies—whether focused on boundary or bioregion detection—typically address the environmental or historical factors that underpin the distribution of identified or inferred boundaries. This is most often achieved by interpreting results within a (palaeo)biogeographical context, for instance, referencing known features such as oceanic circulation patterns, mountain ranges, facies changes, or climatic variability derived from other studies. A less common, but potentially powerful alternative, is the use of quantitative boundary coincidence analysis.

Fortin et al. (1996) introduced four statistics for evaluating the spatial overlap and relative distances between boundaries, along with a permutation-based procedure to assess the statistical significance of these statistics. The most intuitive of these is the boundary overlap statistic, which calculates the proportion of shared boundary elements (BEs). A boundary element is defined as a location exhibiting a statistically significant turnover rate; linking adjacent BEs yields a statistically significant boundary. In their study, Fortin et al. (1996) employed triangular wombling to identify BEs across multiple variables, all sampled at identical spatial locations. This consistent sampling design enabled a direct comparison of boundary overlap.

However, in studies where variables are measured at different locations, such direct comparisons may not be feasible. For such cases, the remaining three statistics proposed by Fortin *et al.* are more applicable, as they rely on spatial distances between boundaries. The first two statistics assume a directional relationship, calculated by measuring the average minimum distance from the BEs of one boundary to those of another. The third statistic is symmetric, obtained by averaging the previous two.

Kent et al. (2006) caution that boundary coincidence analysis remains in its infancy, and methodological challenges persist. Nonetheless, promising applications have emerged (e.g. Davis & Gagné, 2018), indicating that the field holds potential. As such, boundary coincidence analysis offers a promising direction for developing more statistically robust explanations of boundary and bioregion distributions. Future developments are likely to incorporate uncertainty estimates within detected boundaries, potentially leveraging advances in Bayesian wombling and related methodologies.

2.2.4. Summary

Boundary detection methods represent a possible alternative to bioregionalisation approaches aimed at identifying bioregions. Rather than focusing on the bioregions themselves, these methods emphasise what lies between them—namely, biotic boundaries, or zones of rapid and statistically significant biotic turnover. However, these approaches often yield open boundaries. While identifying areas of concentrated biotic turnover is undoubtedly useful, open boundaries pose difficulties when delineating spatially contiguous bioregions. Such delineations are typically required for bioregionalisation and mapping purposes, or to meet the input criteria of other methodological tools that rely on coherent spatial units.

Deriving bioregions from open boundaries would require extending and connecting the identified boundaries through areas where the presence of localised, statistically significant biotic turnover is not supported by data. As such, boundary detection methods such as wombling and split moving-window (SMW), despite their significant advancements over the years, have limited capacity to fully replace bioregionalisation methods in the task of delineating bioregions via established boundaries. SMW, in particular, requires the tuning of multiple parameters and yields only 0D boundaries (i.e., points on a transect), whereas wombling identifies local boundaries, the scale of which may only be cumbersomely increased by spatially aggregating data.

Nonetheless, boundary detection and analysis methods have seen considerable improvement and, in some respects, now surpass bioregionalisation approaches. For example, wombling has already been extended into the spatiotemporal domain, producing 2D boundary surfaces (Halder, 2020; Halder et al., 2024) and it now supports functional data (Barratt & Aston, 2025). To my knowledge, no current bioregionalisation methods operate directly within a spatiotemporal framework to yield 3D bioregions, nor do they support functional data.

In other respects, parallel developments can be observed across the two methodological domains. Boundary detection methods have increasingly incorporated statistical techniques to evaluate boundary significance and probability, such as Monte Carlo and Bayesian approaches. Similar objectives can be seen in bioregionalisation studies through the development of techniques such as ANOSIM.

In conclusion, while traditional bioregionalisation methods remain better suited to identifying spatially contiguous bioregions, boundary detection and analysis techniques provide valuable complementary insights. Rather than serving as alternatives to bioregionalisation, these tools are best regarded as supplementary approaches that enhance our understanding of the spatial and temporal dynamics of biotic turnover. For instance, boundary coincidence analysis can be effectively applied for similar goals as in boundary analysis to the boundaries of bioregions delineated through bioregionalisation methods, while techniques such as wombling or split moving-window (SMW) analysis can be employed to validate those boundaries and to highlight areas where biotic turnover is particularly concentrated.

2.3. Historical Biogeography Methods

Methods that analyse and reconstruct the historical distributions of taxa occupy an intersection between historical and evolutionary biogeography, as they integrate evolutionary information (e.g. phylogenetic trees). These approaches are essential for understanding aspects of the spatial and temporal organisation of biota that are not captured by the methods already discussed. While the latter methods reveal spatial structures within biota, approaches that reconstruct historical distributions can elucidate how these structures have evolved over time. This is because changes in the spatial organisation of biota are, essentially, emergent effects of shifts in the distributions of various taxa. The identification of large-scale dispersal and vicariance events—linked to specific geological, climatic or ecological phenomena—can indicate significant biotic spatial restructuring events and their causes. Conversely, if a spatial restructuring event has been mapped and is well understood (for example, using the methods discussed above), then reconstructing the associated dispersal, vicariance, speciation, and extinction events can illuminate the environmental and ecological processes that led to the event, as well as identify taxa groups that contributed most significantly.

Bretskyan hierarchy theory also highlights the importance of large-scale interactions among Bretskyan entities, shaped by biotic interchange events that involve migrations, and subsequent extinctions driven by competition (Spiridonov & Eldredge, 2024). Considering the long-term effects of these processes on the survival and evolution of Bretskyan entities leads to significant concepts such as the fitness of these entities (Spiridonov & Eldredge, 2024). However, bioregionalisation methods that focus solely on revealing the spatial organisation of biota and its temporal changes (for instance, by analysing spatial structuring across series of time bins) fall short of clarifying these broader interactions or the roles that particular taxa may play in them.

In this section, historical biogeography methods will be reviewed. Despite the relative youth of the discipline, the methodologies employed have a considerable history. Many of the most popular methods currently in use were inspired by earlier approaches and by recognising their limitations. Consequently, since these legacy methods are foundational and even continue to be applied to some extent today, it is worthwhile to begin the overview by discussing them. Accordingly, this section is divided into two parts: Legacy Methods and Recent Methods.

2.3.1. Legacy Methods in Historical Biogeography

Morrone and Crisci (1995) overviews five methods in historical biogeography:

1. Dispersalism,
2. Phylogenetic biogeography,
3. Panbiogeography,
4. Cladistic biogeography,
5. Parsimony analysis of endemicity.

Since then, the use of these methods has declined due to the emergence of model-based, quantitative historical biogeography approaches. However, their foundational ideas and principles remain important since they served as a basis for methodological advancement, and most of these methods are still applied to this day, although with a lesser frequency (Fig. 17).

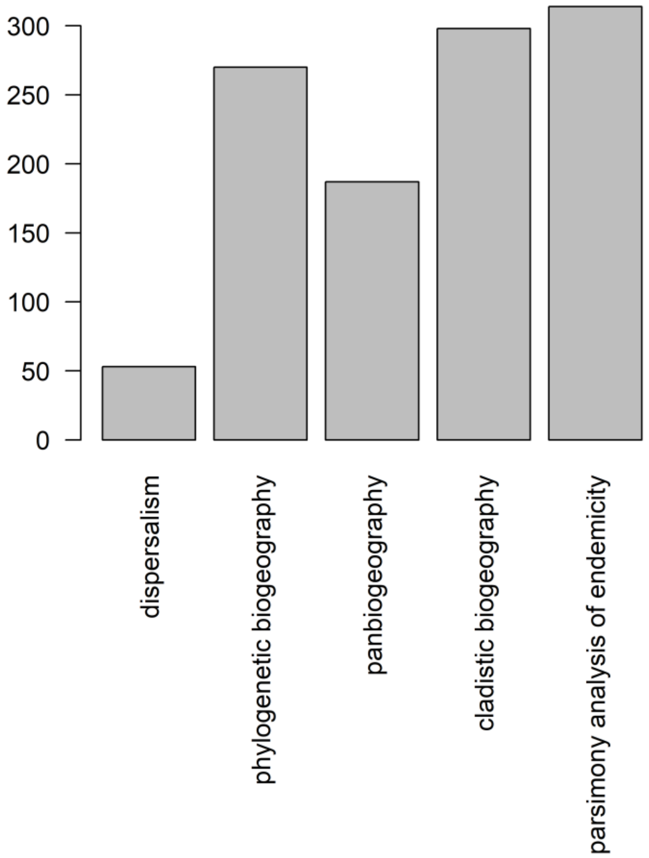


Figure 17. Number of Google Scholar search results (last checked on 12 March 2025) for the phrase '"X" "biogeography"'—where X is the method's name—restricted to publications from 2020 onwards. The restriction was used to reflect contemporary trends.

Parsimony Analysis of Endemicity has already been described in the previous section as a method for identifying areas of endemicity, along with a discussion of its suitability for inferring historical biogeographical patterns. Please refer to that section for further details on this approach. In the following subsections, the four remaining methods will be briefly summarized.

Dispersalism

Dispersalism, which emerged in the 1950s, can be regarded as the most rudimentary and descriptive method for interpreting historical biogeographical patterns, drawing primarily on the ideas first put forward by Charles Darwin and Alfred Russel Wallace (Morrone & Crisci, 1995). It is based on the perspective that new, more derived species originate in a centre of origin—akin to a "Garden of Eden"—and then disperse outward, thereby displacing more primitive forms. Central to dispersalism is the identification of this centre of origin using predefined criteria, where one expects to find the oldest fossils of the most primitive taxa alongside the youngest fossils, or even extant representatives, of the most advanced taxa (Morrone and Crisci, 1995). In general, dispersalism explains spatiotemporal fossil distribution patterns as the result of a series of dispersal events and extirpations caused by ecological displacement.

However, this approach has been heavily criticised. Notably, it precludes vicariance as a cause for speciation (Morrone & Crisci, 1995). Thus, allopatric speciation—for example, that occurring when populations cross long-established dispersal barriers, are separated by newly formed barriers, or when a species' range expands rapidly leading to speciation at the periphery (e.g. Birzu et al., 2021)—challenges the core assumptions of dispersalism. Consequently, while the dispersalist approach is of historical significance for having laid the foundation for subsequent historical biogeography methods and stimulating debates, its explanatory power in contemporary biogeographical studies is limited. The historical significance of the approach is reflected in the lowest number of Google Scholar search results (Fig. 17).

Phylogenetic biogeography

Phylogenetic biogeography arose in the 1960s from the idea of applying cladistic (phylogenetic) hypotheses to explain biogeographic patterns, representing a conceptual advance over the more descriptive approach of dispersalism (Morrone, 2023; Morrone & Crisci, 1995). Although it still relies on the notion of a "centre of origin" and dispersal as primary drivers of biogeographic patterns, it provides a more explicit evolutionary framing of speciation, accommodating not only dispersal-based mechanisms but also others, with some recognition of vicariance (Morrone, 2023; Morrone & Crisci, 1995). Because phylogenetic biogeography remains in use today (Morrone, 2023) (Fig. 17), it functions as a foundational method that continues to a limited play a role in contemporary historical biogeography.

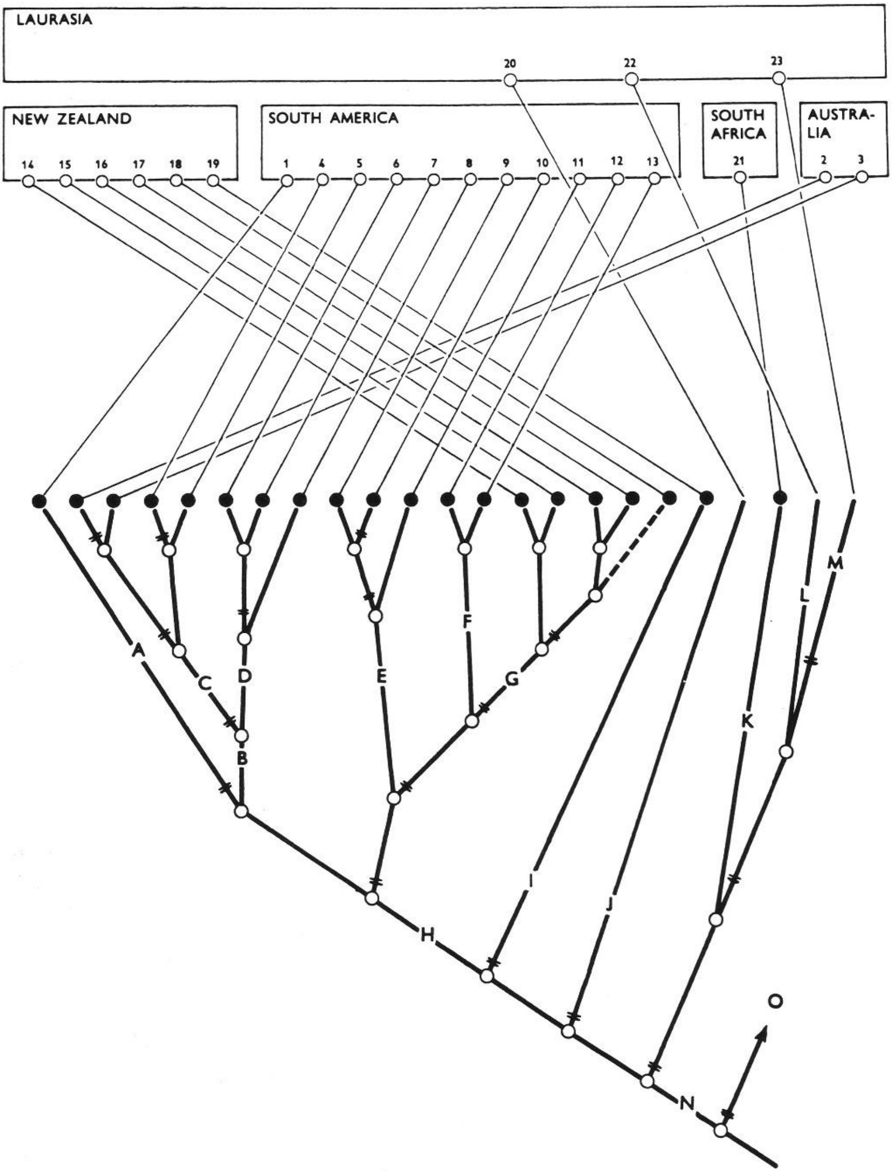


Figure 18. Phylogenetic tree of the Diamesinae and their geographic distribution (Brundin, 1966). Applying a phylogenetic biogeography approach to this pattern led to the interpretation that South America and New Zealand each had separate connections with Antarctica, while South Africa was the first landmass to lose all connections. Additionally, Australia was identified as the centre of evolution (Morrone, 2023). Reproduced from Morrone (2023), licensed under CC BY 4.0 (http://creativecommons.org/licenses/by/4.0/).

In phylogenetic biogeography, it is common practice to visualise phylogenetic trees of monophyletic groups alongside their geographic distributions (Fig. 18). As a result, the method can sometimes be conflated with cladistic biogeography, which places greater emphasis on vicariance and seeks congruent area–phylogenetic patterns across multiple taxa (Morrone, 2023). In contrast to dispersalism, phylogenetic biogeography posits that the most primitive forms remain near the centre of origin, whereas more derived (apomorphic) species emerge at the periphery through dispersal-facilitated speciation. Additionally, it assumes that when two sister species diverge, one deviates more markedly from the ancestor than the others. Both ideas were originally formalised by progression and deviation rules (Morrone & Crisci, 1995). Over time, additional rules have been introduced, relating the phylogenetic relationships of taxa in different locations to biogeographic connections between those areas (e.g. the phylogenetic intermediate rule, the multiple sister-group rule, and the drift sequence rule (Morrone, 2023).

Despite encompassing a broader range of speciation mechanisms, phylogenetic biogeography retains a central focus on dispersal from a centre of origin (or on the connections that enable dispersal), yet it expects a pattern inverse to that described by classical dispersalism.

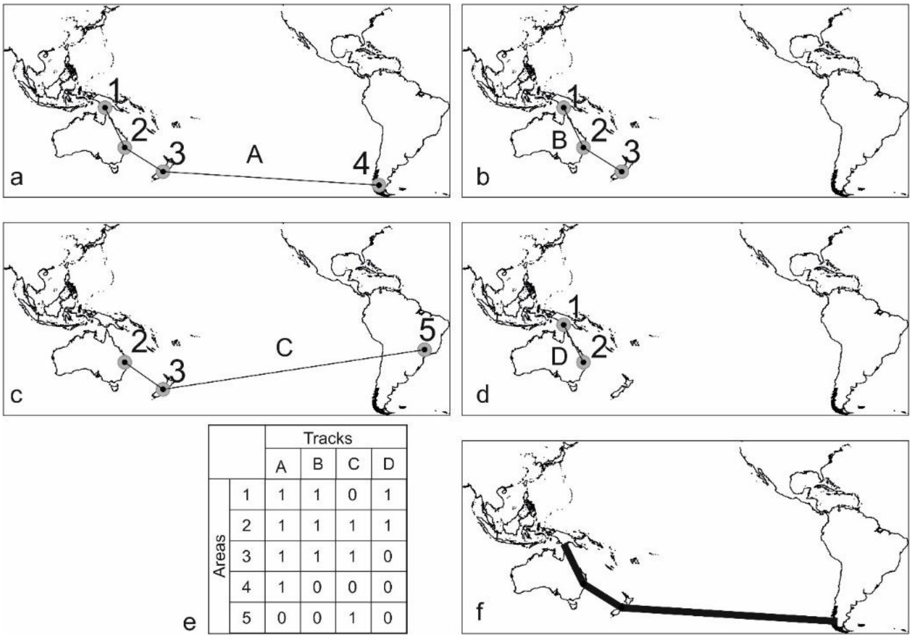
Panbiogeography

Panbiogeography, developed in the late 1950s, initially diverged from other contemporary biogeographical methods by emphasising vicariance in explaining historical patterns (Morrone, 2015; Morrone & Crisci, 1995). Its core procedure involves drawing a minimum spanning tree on a map to connect spatially disjunct fossil localities (or localities for extant taxa). These lines are termed tracks. Next, each track is oriented by adding directional arrows, determined by three possible criteria (Morrone & Crisci, 1995):

- Baseline features – The track crosses tectonic or geographic structures (e.g. mountain ranges, faults, or oceans).
- Main massing – Diversity is concentrated in a particular area.
- Phylogeny – The track runs from sites of more primitive species to those of more derived species.

Notably, orienting a track on the basis of main massing is similar in spirit to assuming dispersal from a centre of origin, as in the two earlier methods. A second major difference from these earlier approaches is that panbiogeography seeks generalised tracks—that is, congruent patterns observed in the tracks of different taxonomic groups. Various quantitative procedures exist to assess the compatibility of tracks across taxa and to identify a generalised track (Fig. 19). Even Parsimony Analysis of Endemicity can be employed for this purpose (Montiel-Canales et al., 2016).

By incorporating these multiple criteria for track orientation, panbiogeography is integrative, accommodating various explanations and evidence. According to its proponents, criticisms stem mainly from inadequate application or misinterpretation (Escalante et al., 2017; Heads, 2015; Morrone, 2015; Morrone & Crisci, 1995). Although many 1980s and 1990s studies relied heavily on vicariance to explain patterns in generalised tracks—incurring criticism—the method has since become more balanced in interpretation (Morrone, 2015). Nonetheless, some critiques remain valid: for instance, its effective use may require taxa with wide ancestral distributions, and it largely overlooks environmental change as a driver of evolution (McGlone, 2016).



		Tracks			
		A	B	C	D
Areas	1	1	1	0	1
	2	1	1	1	1
	3	1	1	1	0
	4	1	0	0	0
	5	0	0	1	0

Figure 19. Tack compatibility analysis (Morrone & Crisci, 1995). From (a) to (d): tracks of different taxa. (e): An areas × tracks matrix, indicating which areas each track passes through. (f): The generalised track derived from the numerical track compatibility analysis. Reproduced and modified with permission from (Morrone & Crisci, 1995). Coastlines data used in reproduction taken from Natural Earth (naturalearthdata.com).

Overall, panbiogeography can be described as a descriptive, spatial, integrative, and semi-quantitative biogeographic approach that infers historical connections by examining spatial congruence among taxa and representing these connections visually. It accommodates a broad spectrum of biogeographic interpretations. While it has lost traction because of accumulated realization of limitations, it remains relevant and is still employed in contemporary biogeography—at least among a portion of the scientific community (Aguilar-Estrada & Morrone, 2022; Allegue et al., 2024; Escalante et al., 2017; Heads, 2015; Morrone, 2015) (Fig. 17).

Cladistic Biogeography

Cladistic Biogeography (CB) emerged in the 1970s as another foundational and the most popular (Fig. 17) legacy approach to reconstructing the historical distributions of organisms. The procedure is relatively straightforward (Morrone & Crisci, 1995; Myers & Giller, 1988):

1. Construct a phylogenetic tree;
2. Encode the distribution of each taxon (e.g. via binary or multistate codes);
3. Map these codes onto the phylogenetic tree.

The outcome is an area cladogram, representing the historical relationships among various regions (Fig. 20). The second step is essential when taxa distributions are complex, i.e. when multiple partial overlaps exist rather than each taxon being confined to a unique area (Morrone & Crisci, 1995). To summarise distributions, methods capable of identifying bioregions or endemic areas—such as endemicity analysis—can also be employed (López-Collar & Escalante, 2024). In CB, congruent splits across unrelated lineages that coincide with geographical breaks are often interpreted as evidence of vicariance (e.g. the emergence of a dispersal barrier or continental fragmentation), although context is crucial for accurate interpretation (Morrone & Crisci, 1995; Myers & Giller, 1988).

Similar to panbiogeography, CB seeks congruent patterns across multiple taxonomic groups, ultimately aiming to produce a generalised area cladogram (Morrone & Crisci, 1995). As noted, CB also parallels phylogenetic biogeography; these two approaches are sometimes conflated because both use phylogenetic trees to explain organisms' geographical distributions (Morrone, 2023). However, phylogenetic biogeography typically focuses on a single taxon, whereas CB—like panbiogeography—aims to identify prevailing biogeographic patterns in entire biotas. Moreover, CB more frequently attributes spatial phylogenetic divisions to vicariance, whereas phylogenetic biogeography often links dispersal to geographic speciation (Morrone, 2023).

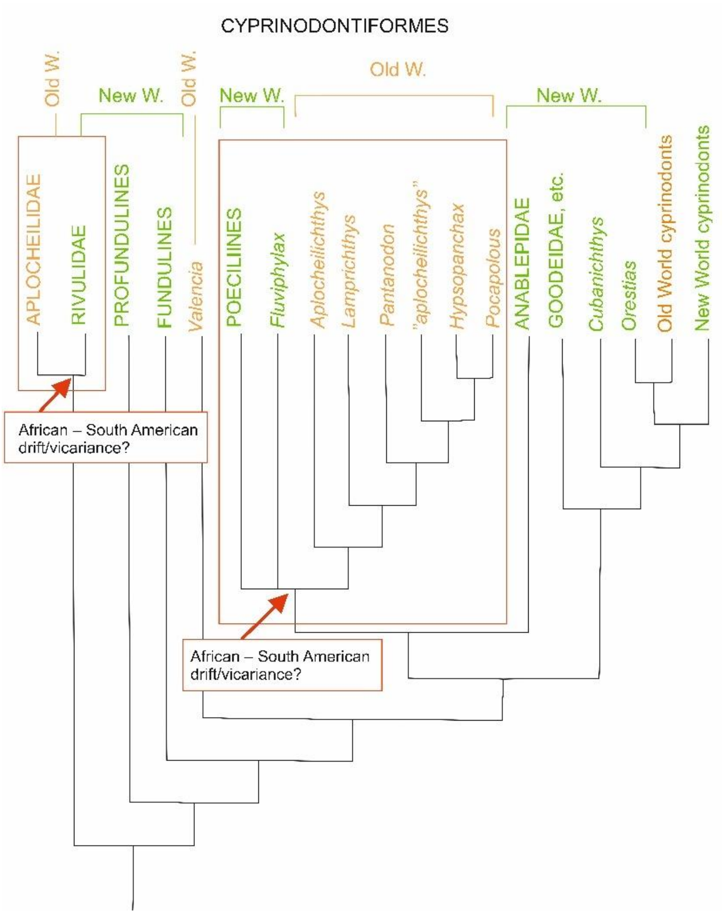


Figure 20. This area cladogram, based on phylogenetic hypotheses by Parenti (1981), illustrates the biogeographic history of Cyprinodontiformes. Red rectangles denote groups whose biogeographic history is best explained by African–South American drift-induced vicariance. In contrast, explaining the biogeographic history of other groups requires the consideration of over-oceanic marine dispersal. For example, while the African–South American separation accounts for the distribution of Poecilidae in South America and Aplocheiloidei in Africa, the occurrence of younger aplocheilid groups outside Africa (e.g. *Pantanodon*) suggests that marine dispersal events have also played a role after the fragmentation of Gondwana (Lundberg, 1993). Figure reproduced and modified with permission from Lundberg (1993).

Like phylogenetic biogeography and panbiogeography, CB remains relevant in contemporary historical biogeography (Frota et al., 2020; García-Navarrete et al., 2023; Hernández Cisneros & Velez-Juarbe, 2021; Morrone, 2023), and there even have been recent efforts to expand and strengthen its methodology (Santos et al., 2023). However, cladistic biogeography is criticized for assuming that all taxonomic groups share a single, vicariance-driven, branching pattern of area relationships. In reality, different groups respond variably to dispersal barriers, whereas endemic area relationship patterns are more network-like (reticulate) rather than strictly branching and hierarchical—partly because dispersal can lead to the recolonization of previously occupied zones (Ronquist, 1997).

Application of CB can be exemplified by a case study of Lundberg (1993), which analysed the historical biogeographic relationships between South American and African freshwater fishes. The similarities between these extant fishes have been noted since the early twentieth century. Following the widespread acceptance of plate tectonic theory, trans-Atlantic biotic relationships—including the observed similarities in freshwater fishes—were largely explained by vicariance-driven evolution resulting from the separation of the South American and African landmasses. However, Lundberg's (1993) study, which employed CB, revealed that the situation is considerably more complex. Many groups of fishes underwent diversification events either before or after the separation of these landmasses. In some groups (e.g. Cyprinodontiformes, see Fig. 20), the observed distribution patterns require the consideration of marine dispersal, whereas in other groups (such as Mormyriformes and Gymnotiformes), the applicability of the drift-vicariance model invokes the assumptions about extirpations.

Summary of classical historical biogeography methods

The classical historical biogeography methods discussed here all incorporate certain expectations about how phylogenetic relationships intersect with geographical relationships. Despite the passage of time, most of these classical methods—including parsimony analysis of endemicity, panbiogeography, and cladistic biogeography (but excluding dispersalism)—remain in use (at least to some extent) in recent historical biogeography studies. Nevertheless, relative to more advanced contemporary methods, they now occupy a somewhat marginal position within the broader field (Fig. 21)

Parsimony analysis of endemicity, panbiogeography, and cladistic biogeography can be applied to polyphyletic groups, thereby revealing congruent biogeographical patterns spanning entire biotas. By contrast, dispersalism and phylogenetic biogeography were originally designed to illuminate taxon-specific biogeographical patterns. Because the first set of methods (i.e. parsimony analysis of endemicity, panbiogeography, and cladistic biogeography) generally places greater emphasis on vicariance and congruent patterns, they align more closely with Bretskyan hierarchy theory, which stresses the role of significant dispersal barriers in shaping biotic structures (Spiridonov & Eldredge, 2024). Consequently, these methods could be employed to discern broad-scale historical relationships among Bretskyan entities, once such entities have been identified through other biogeographical regionalisation methods. In contrast, methods such as phylogenetic biogeography can offer a more fine-grained perspective on the roles of specific taxa.

A shared limitation among these classical approaches is that none of them incorporate rigorous statistical models capable of explicitly handling uncertainties and modelling the evolutionary processes underlying biogeographical patterns. Accordingly, the following section will explore newer methods that address these shortcomings.

2.3.2. Recent Methods in Historical Biogeography

In recent decades, historical biogeography has undergone a surge in methodological advancements, frequently incorporating techniques from fields such as phylogenetics (e.g. character evolution algorithms) and leveraging Bayesian and likelihood-based frameworks. Consequently, modern methods are now far more prevalent in current research than legacy approaches (compare Figs. 17, 21).

Rather than providing an exhaustive review of all recent methods, focus will be put on a selected subset—namely DIVA, DEC, and BioGeoBEARS—as these collectively illustrate the contemporary methodological landscape in historical biogeography. This is not to suggest that these methods are superior, or that they encompass the entire discipline. Other commonly used tools include, for example, RASE (Quintero et al., 2015), BayArea (Landis et al., 2013), and BBM (alongside other RASP software implementations) (Yu et al., 2019; Y. Yu et al., 2015) which also feature prominently in modern practice (Fig. 21).

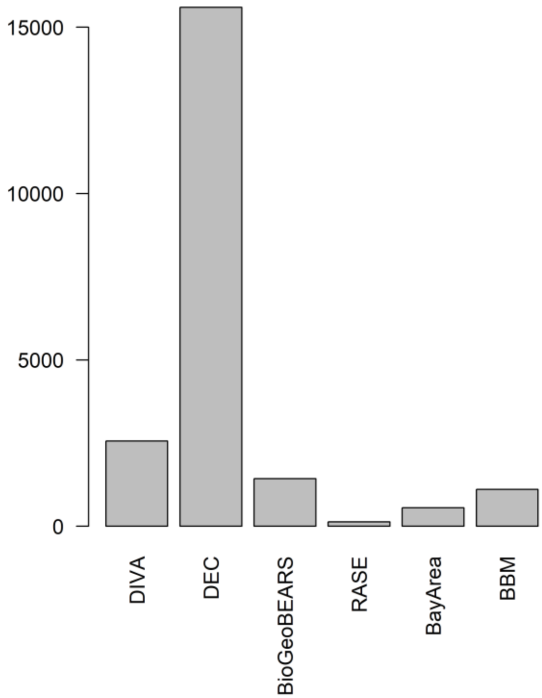


Figure 21. Number of Google Scholar search results (last checked on 12 March 2025) for the phrase '"X" "biogeography"'—where X is the method's name—restricted to publications from 2020 onwards. The restriction was used to reflect contemporary trends. Full names of the methods are Dispersal-Vicariance Analysis (DIVA), Dispersal-Extintion-Cladogenesis modelling (DEC), BioGeography with Bayesian (and likelihood) Evolutionary Analysis in R scripts (GeoBioBEARS), Range Ancestral State Estimation (RASE), Bayesian inference of historical biogeography for discrete areas (BayArea), Bayesian Binary Monte Carlo Markov Chain Analysis (BBM).

Dispersal-Vicariance Analysis

Dispersal-Vicariance Analysis method (DIVA) was proposed as a response to the limitation of methods like cladistic biogeography (CB) (Ronquist, 1997). These methods were criticized because they assume branching, hierarchical patterns in relationships between endemic areas that are common across multiple taxonomic groups or entire biotas. However, relationships between endemic areas are believed to be more of a reticulate nature and different in different groups of taxa, which is assumed by DIVA (Ronquist, 1997).

DIVA was derived from character optimization methods and it is parsimony-based, event-cost-counting method that seeks to identify ancestral ranges with a minimal cost (Ronquist, 1997). Its input requires a fully resolved, rooted phylogenetic tree and a presence/absence matrix indicating distribution of taxa across different geographical areas. Using this data DIVA employs character optimization algorithms to compute costs for events leading to different combinations of ancestral ranges, seeking to find optimal solution with the lowest cost. Each speciation event in DIVA is assumed to be caused either by vicariance events that split ancestral range into two parts or by a particular type of sympatric speciation event (termed 'duplication') where daughter species inherit their ancestral ranges; both these events are cost-free. Whereas the other two allowed events-dispersal and extinction-are assigned a cost of 1. Thus, DIVA favours explanations with maximal vicariance and duplication, and minimum dispersal, and extinction. The output of DIVA contains a list of inferred vicariance, dispersal and extinction events, presented by a geographically annotated phylogenetic tree showing reconstructed geographical ranges (e.g. Fig. 22c-g)

DIVA has been criticized for bias towards all-vicariance explanations, and inability to model range expansions and extinctions (Cáffaro et al., 2022; Díaz Gómez, 2009; Kodandaramaiah, 2010). Furthermore, it does not involve 'subset' sympatric speciation events, where one of the daughter species occupy a fraction of ancestral range, or founder speciation events, where speciation occurs immediately after dispersal in a newly colonised territory. Also, compared to more recent methods, DIVA, like previously presented classical historical biogeographical methods, lacks statistical rigour since it only identifies the most parsimonious, single solution under the given event-cost rules, without estimating uncertainty related to quality of phylogenetic reconstructions and attributing any kind of probabilities or likelihoods to alternative solutions that can be equally or comparably likely (Harris & Xiang, 2009; Nylander et al., 2008; Yu et al., 2010).

As a response to these limitation, Statistical Dispersal-Vicariance Analysis (S-DIVA) method was developed later as an extension of DIVA (Yu et al., 2010), implementing solutions presented by (Nylander et al., 2008) and (Harris & Xiang, 2009). Instead of relying on a single phylogenetic tree topology, that is assumed to be flawless, S-DIVA supports a sample of candidate tree topologies, then applies a modified DIVA approach on each tree to find multiple equally optimal, alternative solutions, ultimately aggregating these solutions across all trees. The result of S-DIVA, therefore, encompass probabilities of alternative ancestral ranges for each ancestral node and contains multiple optimal ancestral range reconstructions (Fig. 22). By being based on multiple bootstrapped or Bayesian tree topologies sampled from posterior distribution, S-DIVA is able to account for phylogenetic uncertainty, while the consideration of equally optimal solutions solves the problem of ancestral area optimization (Yu et al., 2010).

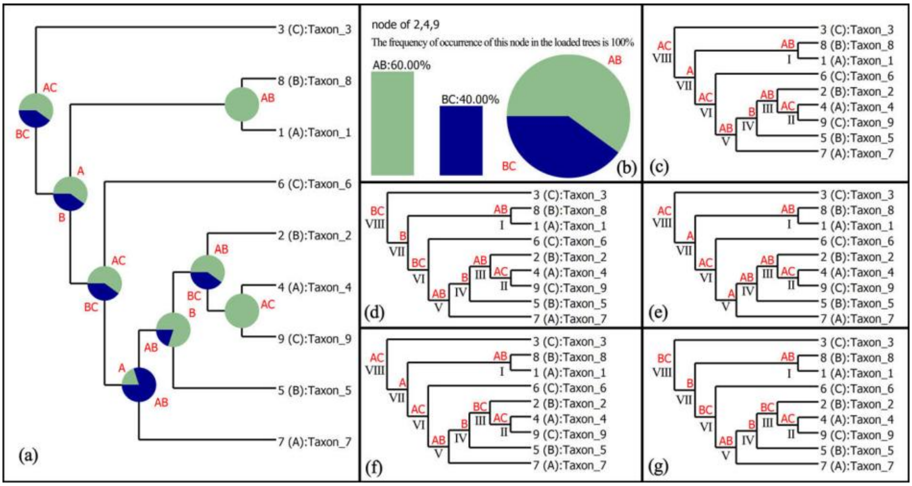


Figure 22. Graphical S-DIVA output as presented in Yu et al. (2010), reproduced with a permission. (a) Ancestral distributions for a simulated 9-species phylogeny across 3 areas (A, B, C), with pie charts showing probabilities of alternative ancestral ranges at nodes. (b) The node ((4,9),2) has two possible ancestral ranges (AB: 60%, BC: 40%), displayed as pie and bar charts in S-DIVA; since the node appears in all trees, its probability is 100%. (c–g) Five optimal reconstructions contributing to the probability estimates in (a) and (b).

Considering that DIVA-like methods (e.g. S-DIVA) are implemented in modern software packages like RASP (Yu et al., 2019; Y. Yu et al., 2015) and R package BioGeoBEARS (Matzke, 2018), and there is considerable number of studies applying them in biogeography (google scholar search with ‘geobiogeography “DIVA”’ yielded ~2500 results for the last 5 years, as of 2025-02-26), DIVA, and its derivations, still play an important in contemporary biogeography.

Dispersal-Extinction-Cladogenesis model

A major step toward more statistically rigorous methodology and a shift away from parsimony-based approaches is the development of the Dispersal–Extinction–Cladogenesis (DEC) model (Ree et al., 2005; Ree & Smith, 2008).

Currently, DEC and its extension dominate historical biogeography research landscape (Fig. 21). Ree et al. (2005) recognised the equivalence between evaluating the likelihood of an organismal trait (character) on a phylogeny, under a specified evolutionary model, and evaluating the likelihood of extant species ranges given their phylogeny and palaeogeographic information. Consequently, they adapted methodologies from character evolution models to the field of historical biogeography.

DEC employs a maximum likelihood framework to model geographic range evolution as a continuous-time Markov process, driven by dispersal (range expansion), extinction (range contraction), and cladogenesis (range inheritance during speciation) events. An earlier method implemented a Monte Carlo approach—simulating these events as outcomes of a Poisson process (Ree et al., 2005)—whereas DEC (Ree & Smith, 2008) provides an analytical and computationally more efficient solution. The following description of the DEC model and its algorithm draws on these two publications and interpretations of the formulas presented therein.

As input, DEC requires:

- A fully resolved, time-calibrated phylogenetic tree;
- Distribution data for the terminal taxa (e.g. a presence/absence matrix of extant species);
- Area definitions, including constraints on valid range combinations (e.g. only adjacent areas may be combined);
- Priors for range inheritance scenarios—specifying how a range can be split or inherited during cladogenesis (commonly a uniform prior is used in implementations (Matzke, 2013), assigning equal probability to each scenario and not favouring any particular biogeographical hypothesis).

In addition, the model requires initial values for its free parameters—namely dispersal and extinction rates for every pair of areas. These rates can be asymmetrical (e.g. to account for prevailing winds or ocean currents). Values for these parameters are then estimated through a maximum likelihood approach, identifying those parameters that maximise the likelihood of the observed data (i.e. the time-calibrated tree and the range distributions of its tips) under the DEC model.

DEC constructs an instantaneous range transition matrix (Q), specifying dispersal rates between areas (upper part of the matrix) and extinction rates for the areas (lower part). The diagonal entries are set so that each row sums to zero. The matrix is assembled to allow only a single change in a range at a time (for instance, the dispersal rate from area A to B and from area A to C may be non-zero if AB and AC are valid ranges, whereas the rate from A to BC is zero even if ABC is viable, because that would require two simultaneous dispersals). In effect, the values in Q represent one-step events or infinitesimal range changes. Using this matrix, range transition probabilities are calculated for each branch and ancestral range in the phylogenetic tree as a function of branch length (t):

$$P(t) = e^{-Qt}$$

Eq. 9

This approach to calculating transition probabilities constitutes continuous-time Markov process modelling, as it sums over the probabilities of any number of these one-step events occurring over a finite branch length. Hence, transitions involving multiple range changes remain possible along the branches. The method is analogous to stochastic Poisson processes for dispersal and expansion, as applied in earlier work (Ree et al., 2005).

DEC calculates the likelihood of observed data by combining its transition probability matrix P(t) with range inheritance scenarios (and their assigned priors), using the Felsenstein's postorder pruning algorithm. At each internal node and for each candidate ancestral range, the method computes a conditional likelihood—the probability of the ranges observed at the tree's tips, given the DEC model and the assumption that this node had range r. Essentially, DEC enumerates all possible ways (e.g. range inheritance scenarios at cladogenesis nodes and range transitions along branches) in which a particular ancestral range r at an internal node n could yield the observed terminal ranges, weighting each path by its probability. This procedure is encapsulated by the equation that calculates the conditional likelihood for an internal node n, assuming the presence of range r:

$$f(n,r) = \sum_{(r_1,r_2) \in S(r)} p_{inh}\left(r \rightarrow \left(r_1,r_2\right)\right) \times L_{n_1}\left(r_1\right) \times L_{n_2}\left(r_2\right)$$

Eq. 10

In eq. 10, $p_{inh}\left(r \rightarrow \left(r_1, r_2\right)\right)$ denotes the prior probability of a range inheritance scenario in which the ancestral range r splits into two daughter ranges, r_1 and r_2. The term $S(r)$ represents the set of all possible ancestral range subdivision and inheritance scenarios for range r. Meanwhile, $L_{n_i}\left(r_i\right)$ is the likelihood contribution from the branch leading to the daughter node n_i, given that immediately after cladogenesis, node n had the range r_i (where i is either 1 or 2). The likelihood contribution of a branch leading to a daughter node is then calculated as follows:

$$L_{n_i}(r_i) = \sum_{s_i} P_{r_i, s_i}(t_i) \times f(n_i, S_i)$$

Eq. 11

In eq. 11, s_i denotes the range after a time interval of length t_i (the branch length). $P_{r_i, s_i}(t_i)$ is the range transition probability from the parent node n having range r_i to the daughter node n_i having range s_i, and depends on the branch length as well as the dispersal and extinction rate parameters. Finally, $f(n_i, s_i)$ represents the conditional likelihood of the daughter node n_i, given that range s_i is present at n_i.

The last term $f(n_i, s_i)$ reflects the recursive nature of the postorder algorithm. It calculates conditional likelihoods for every possible range at each internal node, beginning from the tips and then working upward through the tree. At the tips, $f(n_i, s_{obs})$ is set to the prior probability of the observed range s_{obs} (e.g. *1* if the observed data are considered certain, otherwise *0* for unmatched ranges). Consequently, at the first internal node, just above the tips, $L_{n_i}(r_i)$ reduces to $P_{r_i, s_{obs}}(t_i) \times f(n_i, s_{obs})$, which—if $f(n_i, s_{obs}) = 1$—simply becomes $P_{r_i, s_{obs}}(t_i)$.

The computed conditional likelihoods, $f(n, r)$, for each range r at every internal node are then stored and reused as $f(n_i, s_i)$ when evaluating $L_{n_i}(r_i)$ for nodes farther from the tips. Eventually, the root node is reached, yielding $f(root, r)$ values for each range r. At that point, the total likelihood of the observed data is computed by integrating across the range priors $P(r)$ and their corresponding conditional likelihoods at the root:

$$L = \sum_{r} P(r) \times f(root, r)$$

Eq. 12

Standard maximum likelihood optimisation techniques can then be employed to find the extinction and dispersal rate parameters that maximise $\boldsymbol{L}$. With these parameters identified, the conditional likelihoods at each node can be normalised, thereby yielding posterior probabilities for the different ranges. This process generates a probabilistic reconstruction of ancestral ranges (Fig. 23).

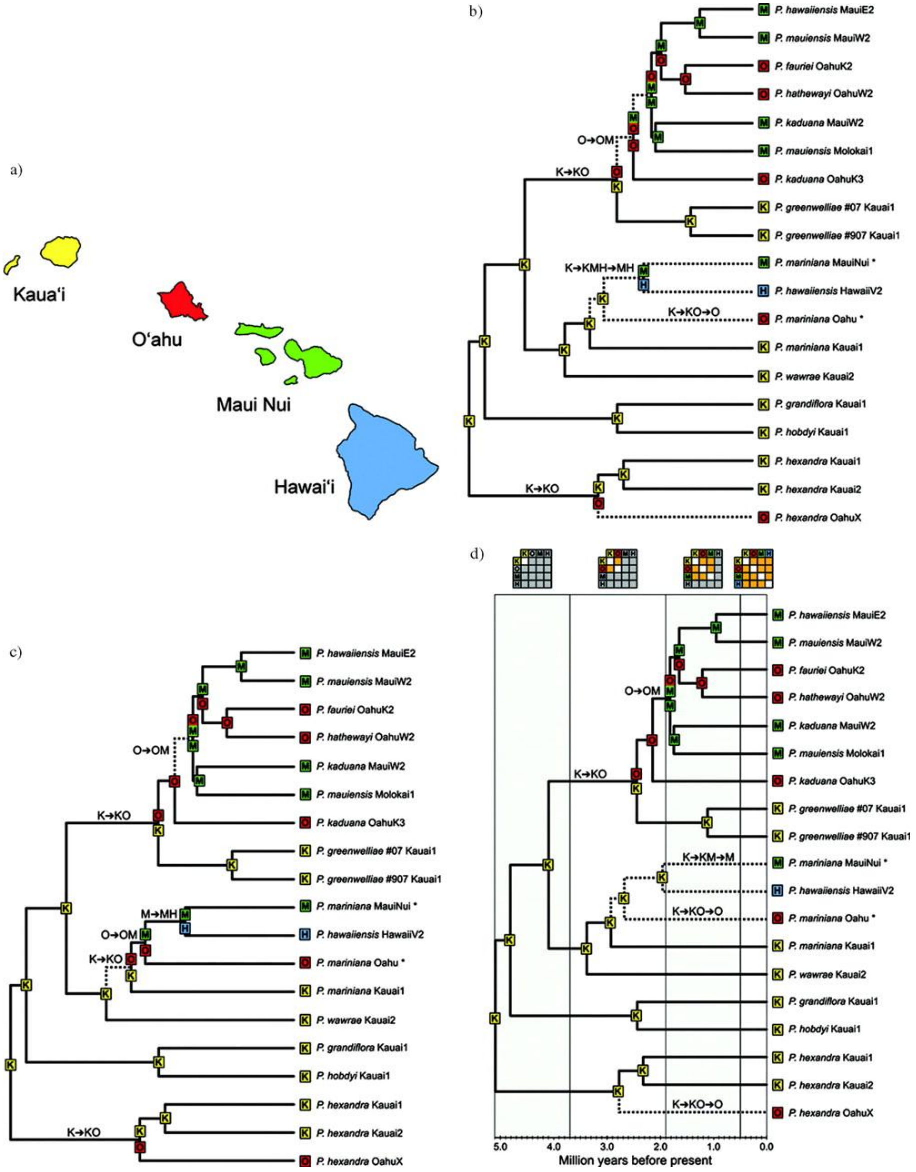


Figure *23*. Example output from a DEC analysis in an empirical case study investigating the historical biogeography of *Psychotria* in the Hawaiian Islands. (A) Map showing the islands included in the study. (B–D) Ancestral range reconstructions: (B) using an unconstrained DEC model; (C) using a constrained DEC model, allowing only eastward dispersal and restricting area definitions to combinations of up to two adjacent islands, this model yielded the highest likelihood; and (D) using a temporally stratified DEC model, constrained according to island origination times. Above the area cladogram are the corresponding Q matrices used for each temporal stratum; grey cells indicate impossible range transitions to or from islands that had not yet formed. Reproduced with permission from *Ree and Smith (2008)*.

DEC can also be employed with a high degree of flexibility, incorporating various constraints and external information as demonstrated by Ree and Smith (2008) and discussed by Ree et al. (2005). For instance, dispersal rates to certain areas might be adjusted using geological or palaeontological evidence (e.g. nullified before times of the origination of a volcanic island, as in Ree and Smith (2008), Fig. 23D) . Likewise, dispersal rates can be constrained to favour specific directions or destinations (e.g. Fig. 23C, (Ree & Smith, 2008). Additional free parameters—such as the timing of barrier or corridor formation—may also be introduced, and comparative analyses across clades with distinct physiological traits can be conducted to test various palaeobiological hypotheses related to dispersal capabilities (Ree & Smith, 2008).

Despite its relatively sophisticated framework, DEC still has limitations. Simulation-based tests suggest that DEC tends to underestimate both dispersal and extinction rates, particularly extinction (Ree & Smith, 2008). In addition, the accuracy of ancestral range reconstructions declines as the ratio of dispersal and extinction rates to speciation increases (Ree & Smith, 2008).

A plausible explanation for this pattern is that higher rates of biogeographical processes, coupled with long temporal windows for range transitions (arising from low speciation rates and the resulting long branches), permit a wider array of potential biogeographical scenarios. Consequently, the relative likelihood of any single observed scenario diminishes under these faster rates. Conversely, fewer changes along shorter branches restrict the range of plausible developments, resulting in a higher relative likelihood of each scenario. Comparable effects of "likelihood dilation" (in unconstrained models) and "likelihood concentration" (under stronger constraints) have been observed when removing or retaining scenarios inconsistent with the data (e.g. the unconstrained M0 model vs. constrained M1/M2 models in Ree and Smith (2008), Fig. 23B-D).

Thus, although DEC's maximum likelihood approach departs significantly from parsimony-based methods like DIVA, it still favours simpler biogeographical explanations—involving lower dispersal and extinction rates—over more complex scenarios.

One further issue with DEC, connected to the previously mentioned tendency to underestimate biogeographical rates, is that there is no guarantee the maximum likelihood solutions are stable or unique. Reconstructions arising from parameter sets with slightly lower but still comparable likelihoods could yield different conclusions. For instance, Ree and Smith (2008) noted that in an empirical case study, different models suggested alternative inheritance scenarios for certain internal nodes. Furthermore, the stratified model (constrained by island origination times; see Fig. 23D) emerged as the least likely—potentially reflecting either inaccurate point estimates of island formation dates, or indicating that DEC's maximum likelihood solution, which underestimates rates of dispersal and extinction, diverges from complex developments that actually took place.

A worst-case scenario would be a flat likelihood distribution in which the maximum likelihood estimate (MLE) model is only marginally more likely than its alternatives. Supporting this concern, Matzke (2014) conducted numerical experiments by varying dispersal and extinction rates in simulated data, finding that under high rates of these processes, the likelihood gap between different models narrowed. In other words, if biogeographical turnover is rapid, multiple explanations tend to become roughly equally likely. Given DEC's tendency to underestimate true rates, it is wise to explore alternative solutions—especially those involving higher parameter values—and, in general, to carry out sensitivity analyses probing how parameter choices affect range reconstructions. Where feasible, prior information on observed biogeographical rates in nature could also be used to inform the model.

Finally, like DIVA, DEC restricts the set of possible speciation scenarios. In DEC, one of the daughter species is necessarily confined to a single area, meaning that a vicariance event splitting an ABCD range into AB and CD—permitted in DIVA—cannot occur in DEC. Moreover, DEC does not support founder-event speciation, under which speciation occurs immediately following dispersal to a new area. The importance of founder-event speciation, especially in island systems, has been demonstrated by model extensions incorporating this mechanism (e.g. DEC-J; (Matzke, 2013; Matzke, 2014). However, these problems with inheritance scenario possibilities are solved by further developments and method extensions (e.g. DEC, DIVA implementations in BioGeoBEARS).

Despite these constraints, the DEC framework remains a state-of-the-art approach and is likely the most popular method in historical biogeography (Fig. 21). It serves as a robust foundation for further methodological developments, including the aforementioned DEC-J.

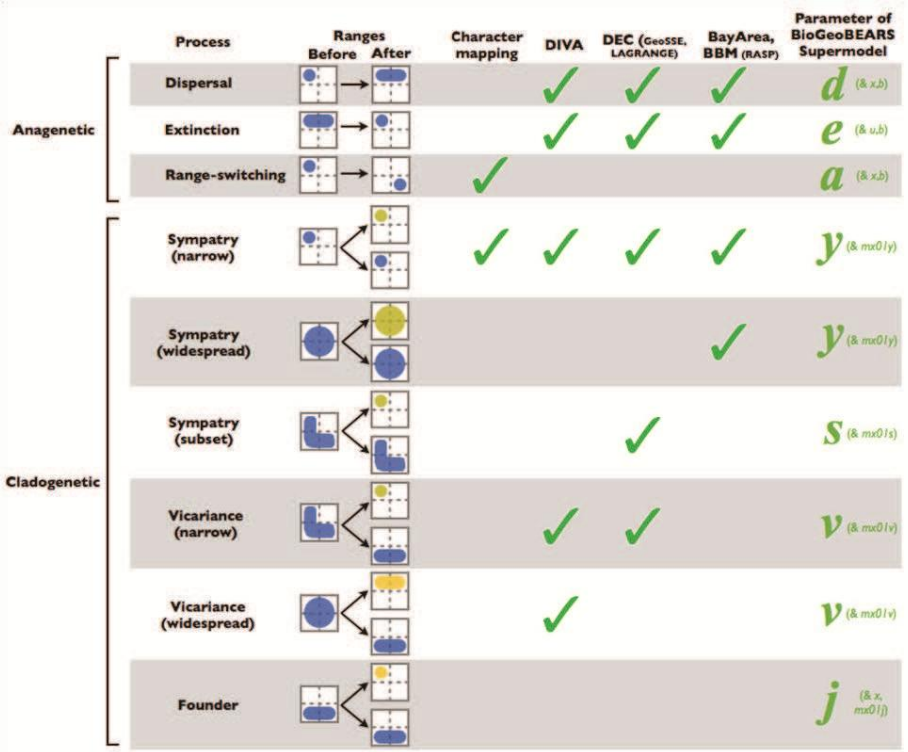


Figure 24. Illustration of the different cladogenetic and anagenetic biogeographical processes assumed by various models, together with the parameters controlling these processes in the BioGeoBEARS supermodel. Reproduced form Matzke (2013), licensed under CC BY 4.0 (http://creativecommons.org/licenses/by/4.0/).

BioGeoBEARS

The next milestone achievement in the science of historical biogeography, following the development of statistically rigorous, probabilistic approaches, is BioGeoBEARS (**BioGeo**graphy with **B**ayesian (and likelihood) **E**volutionary **A**nalysis in **R** **s**cripts). It is an R package developed by Matzke (2013). BioGeoBEARS integrates recent, frequently used historical biogeography methods (or their extensions) under a unified likelihood framework, making it a platform for advanced historical biogeographical studies. It contains BioGeoBEARS supermodel, which uses a list of free parameters controlling biogeographical processes assumed by different methods (Fig. 24). Turning these parameters on or of essentially means switching between different models. The values for these parameters can be estimated using maximum likelihood approach. Thus, by finding which model (or a combination of parameter values) fits data the best, BioGeoBEARS allows to test competing biogeographical hypotheses, and differentiate between essential and non-essential biogeographical processes in each study case (e.g. Matzke, 2014). BioGeoBEARS also implements a parameter controlling founder event speciation – an important, but usually overlooked macroevolutionary, biogeographical process by other methods (Matzke, 2013; Matzke, 2014). In addition, BioGeoBEARS allows to incorporate fossil data to constrain reconstructed ancestral ranges and to account for imperfect detection of species' fossils.

2.3.3. Summary

Over the past century, historical biogeography methods have undergone remarkable advancements. Beginning with rule-based and area-cladogram or track-based explanations, transitioning through a parsimony-based paradigm, these methods achieved statistical rigour in the 2000s—culminating in Bayesian, likelihood frameworks that enable researchers to test and compare the fit of competing biogeographical hypotheses. Yet, there remains scope for further refinement, particularly by drawing on approaches from the biotic regionalisation domain.

Most popular historical biogeographical methods (e.g. DEC, S-DIVA, and the BioGeoBEARS supermodel) depend on discrete area definitions. While this is relatively straightforward in island settings, it becomes far less obvious within a single continent. Herein lies a promising avenue for integrating historical biogeography with bioregionalisation methods and the Bretskyan hierarchy theory framework. For instance, delineating within-continent geobiomes—and tracing their evolutionary history—could help define the areas used in models such as DEC or S-DIVA. Subsequent insights into the historical biogeography of taxa within these geobiomes might then deepen our understanding of evolutionary history of geobiomes and the particular roles of dispersal barriers partitioning them.

2.4. Summary

This overview of methods for studying the spatiotemporal organisation of biota is by no means exhaustive; many additional approaches—such as species distribution modelling (Daumantas, 2022; Daumantas et al., 2020)—could also have been included. Nevertheless, no single method reviewed here, or elsewhere, can fully capture the complexity of spatiotemporal biotic organisation, particularly in contexts that require spatial contiguity, hierarchical structure, and macroecological, historical interpretability.

Instead, each method contributes a distinct piece to the puzzle. Bioregionalisation techniques excel at delineating regional biotic patterns; boundary detection methods identify zones of sharp biotic turnover; and historical biogeographical approaches provide insights into the temporal evolution of biotic spatial structuring and the roles played by particular taxa. Together, these approaches form a complementary suite of tools, offering partially independent perspectives to the same data source. Their integrated applications—when guided by the theoretical framework of the Bretskyan hierarchy—has the potential to yield a robust and nuanced understanding of how biotic entities such as geobiomes form, shift, and persist across space and time. However, such integrated applications could become overly complex and rarely achievable within the scope of standard research practice. This challenge highlights the need for new methodologies specifically tailored to detect and characterise the spatiotemporal biotic structures anticipated by Bretskyan hierarchy theory. The following section introduces one such candidate methodology: HespDiv.

3. HESPDIV FRAMEWORK

The previous section provided an overview of various methods and paradigms used to study the spatiotemporal organisation of biota. It concluded that, for practical reasons, methods aimed at identifying bioregions are often preferred over those focused on detecting boundaries. However, no existing bioregionalisation method appears well suited to identifying the kinds of structures envisioned by Bretskyan hierarchy theory. In particular, current methods often underperform with respect to one or more of the following key qualities: (1) the explicit detection and delineation of hierarchical boundaries in both spatial and temporal domains; (2) the generation of spatially contiguous bioregions; (3) the straightforward interpretability of division strength in terms of an ecological (dis)similarity metric; and (4) flexibility in terms of input data, such as the ability to accept raw occurrence data instead of requiring a sample-to-sample distance matrix.

Ideally, a new method should incorporate all of these features. Furthermore, it would gain a competitive advantage and have greater potential for widespread adoption—and consequently more rapid development—if it supported multiple subdivision criteria (e.g. minimum bioregion area or minimum number of samples per bioregion) and multiple subdivision methods (i.e. alternative approaches for comparing bioregions and processing data, rather than being restricted to a predefined set of (dis)similarity metrics). When combined with flexibility in supported input data formats, such a method would be applicable to virtually any type of patch-based, nested hierarchical system (see section *The Apparent Order of Patches and Smoothness, and Entities as Patches*). A methodological family that fulfils these criteria—**Hie**rarchical **Sp**atial **D**ata Sub**div**ision (HespDiv)—and its specific implementations, *hespdiv* and *birese*, is presented in this chapter of the thesis, together with the corresponding software: the R package “hespdiv”, in which the *hespdiv* method is implemented. Thus, this chapter of the thesis is dedicated to tasks 3–6 (see Introduction). The effectiveness of the developed methods is demonstrated by the results of two case studies (task 6).

3.1. Characteristics of HespDiv Family Methods

Any method possessing the following features may be considered a member of the HespDiv family:

1. The method recursively partitions input data into two spatially contiguous subsets based on boundaries explicitly defined in space, time, or the spatiotemporal domain, in order to generate subdivisions that form a compositional spatial, temporal, or spatiotemporal hierarchical structure. In this structure, each higher-order subdivision constitutes a strict subset of its corresponding lower-order subdivision. Thus, the aim of the method is to produce a temporal, spatial, or spatiotemporal dendrogram.
2. A key input to the method—defining the subdivision strategy—is the comparison function, which determines how spatial, temporal, or spatiotemporal data subsets are evaluated against one another. This function accepts two data subsets and returns a comparison value (e.g. a measure of similarity, dissimilarity, or another metric), which is used to assess the quality of a given subdivision. The comparison function ultimately governs how boundaries are tested and selected, and what type of input data the method can accommodate. This modular design means that each HespDiv implementation can be highly versatile, supporting a range of data types, structures, and subdivision strategies.
3. The method dynamically adjusts its scope and scale during operation. This means that the algorithm either recursively or iteratively applies the comparison function at varying scales, rather than identifying all subdivisions in a single step. This feature ensures that the resulting subdivisions are specific to their respective scales and hierarchical levels, allowing the detection of features that emerge only at particular stages within the hierarchy.

4. The resulting subdivisions are expressed through boundaries (*sensu lato*), which may be 0D, 1D, or 2D, delineating partitions in time/spatial transect, space, or spatiotemporal volume, respectively. These boundaries, along with their hierarchical structure and assigned comparison values, constitute a key output of the method. A HespDiv method systematically evaluates alternative boundary sets, selecting those that optimise the subdivision according to the specified comparison function. The dimensionality of the boundaries, as well as the manner in which they are constructed, evaluated, and optimised, may vary between HespDiv implementations.
5. The identified boundaries define two further key outputs: HespDiv clusters (data groups delineated by the boundaries) and their corresponding spatial, temporal or spatiotemporal domains. The representation of HespDiv domains depends on their dimensionality—for instance, in spatial subdivisions, domains would be represented as polygons; in temporal subdivisions, as time intervals. HespDiv domains are defined by their boundaries, whereas HespDiv clusters are characterised by their associated data points.

These characteristics define a potentially broad family of methods. At first glance, certain clustering approaches—particularly spatially or stratigraphically constrained variants—may appear to qualify as HespDiv methods, as they too aim to generate compositional hierarchies represented by spatial or temporal dendrograms. However, such similarities are limited to their overarching objective. Clustering methods typically do not use, nor produce, boundaries explicitly defined in space or time. Its output is restricted to data clusters and dendrogram revealing their relationships. Moreover, instead of accommodating a wide variety of input data types and employing a comparison function to guide subdivisions, cluster analyses operate on a fixed distance matrix and rely on a linkage function, which is far narrower in scope than a comparison function.

Paradoxically, two methods that come closer to aligning with the HespDiv framework are: the machine learning method known as Classification and Regression Trees (CART) (Breiman et al., 1984), typically used to build explanatory models, and the hierarchical application of the split moving-window (SMW) technique, identifying boundaries along a spatial or stratigraphic transect (Cornelius & Reynolds, 1991; László et al., 2014). CART recursively partitions the input dataset along the axes of explanatory variables that yield the most effective splits. In atypical applications where the explanatory variables are spatial or temporal coordinates, CART may appear similar to HespDiv approaches (eg. Gaudart et al., 2015), as it emphasises and outputs partitions (boundaries), dynamically adjusts its scope through recursive operation, and produces a dual output: data clusters and their corresponding spatial or temporal domains defined by those partitions. However, in standard implementations, partition performance is evaluated not via a user-defined comparison function, but by reductions in Gini impurity (for classification trees) or mean squared error (for regression trees). Although the "rpart" R package (Therneau & Atkinson, 2023), which implements CART, allows users to define a subdivision method via a list of functions—somewhat analogous to the HespDiv comparison function—this is rarely used in practice. Moreover, standard CART applications typically use explanatory variables other than geographical and temporal coordinates, and results are visualised as decision trees, which are less intuitive for spatial or temporal bioregionalization. Thus, while CART resembles the HespDiv framework in certain respects—and some of its modified applications via the "rpart" package could arguably qualify as HespDiv cases—its primary focus on non-spatial and non-temporal partitions ultimately places it outside the HespDiv family.

Hierarchical SMW, on the other hand, appears to possess nearly all the defining characteristics of a one-dimensional HespDiv method (for a detailed explanation, see the Split Moving-Window section). It seeks to produce a hierarchical subdivision of a spatial or temporal transect using 0D boundaries and supports multiple functions for comparing data on either side of the split window. These features make it a strong candidate for inclusion within the HespDiv family. However, it lacks dynamic adjustment of scope and scale, which are fixed by the moving window's width. The SMW profile is generated once, and subsequent subdivisions are placed on increasingly lower peaks in the difference values (Cornelius & Reynolds, 1991), rather than being recalculated at each hierarchical level.

Therefore, to date, only two methods can be confidently classified within the HespDiv family: *hespdiv* (hierarchical spatial data subdivision—the first formal HespDiv method) (Daumantas & Spiridonov, 2024b) and *birese* (binary recursive segmentation) (Rinkevičiūtė et al., 2025). Both methods were developed as part of this thesis and will be introduced in the following sections.

3.2. HespDiv Methods

In this section, two novel methods belonging to the HespDiv family—*hespdiv* and *birese*—are presented, along with the "hespdiv" R package

(Daumantas, 2024) that implements *hespdiv* method. In the following section, their application cases will be presented. Their potential to distinguish Bretskyan hierarchy entities is then discussed in the subsequent section. Finally, planned updates and future prospects for the HespDiv family of methods are outlined in the last section before conclusions.

3.2.1 *hespdiv*

The first HespDiv method developed during the course of this thesis is *hespdiv*, it is presented and reviewed in detail in Daumantas and Spiridonov (2024b). It can be classified as a machine learning, data exploration, and spatial analysis method. Its primary aim is to hierarchically subdivide data in space by optimising the output of a comparison function, thereby producing a compositional hierarchy of spatially contiguous data clusters and their corresponding polygons—essentially a spatial analogue of a dendrogram. The principal inputs to *hespdiv* are: (i) the dataset to be subdivided, (ii) a comparison function (optionally accompanied by a generalisation function), and (iii) subdivision criteria that specify when the recursive partitioning should stop. The data must be represented as points in space (e.g. raster cells or polygons can be represented by their centroids). The general workflow of *hespdiv* algorithm follows a straightforward procedure consistent with the HespDiv family framework:

1. Construct a set of boundaries that spatially divide the data and its bounding polygon into two parts.
2. Evaluate each boundary using a predefined comparison function and select the best performing boundary to establish the subdivision.
3. Repeat steps 1–2 for the resulting polygons and data subsets until stopping criteria are met.

As will be demonstrated later, this generalised procedure closely resembles the operational logic of *birese*. However, the devil is in the detail: the manner in which each step of this general workflow is implemented distinguishes between different HespDiv applications. A more detailed workflow of *hespdiv* is illustrated in Fig. 25.

Boundary construction

hespdiv is designed to generate two types of boundaries: linear and nonlinear. Linear boundaries are simple straight lines in the Euclidean sense (though not necessarily so in geographic terms, due to distortions introduced by geographic projections). Their primary advantages lie in faster computation and producing less complex outputs, which are typically easier to interpret. However, in many cases, real-world boundaries may be poorly represented by straight lines. In such instances, nonlinear boundaries offer a distinct advantage. These are constructed as splines, exhibiting variable slope and more intricate, wavy, or sinusoidal forms (e.g. Fig 25 step 4) that may better align with the spatial discontinuities present in the data.

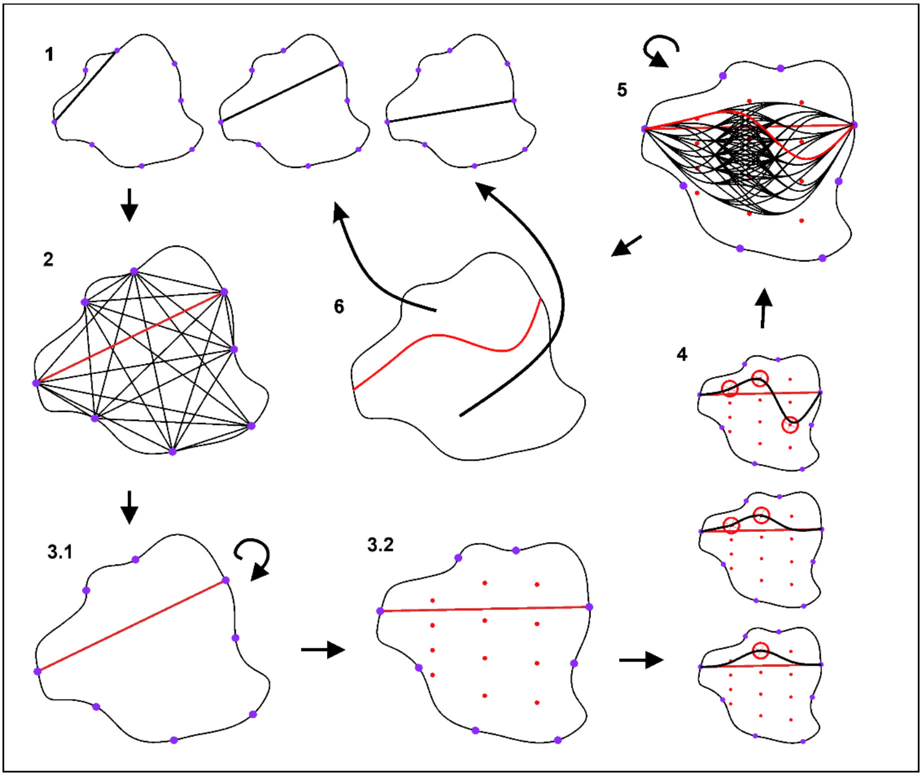


Figure ***25***. Visual workflow of the hespdiv algorithm process: (1) Construct multiple linear split-lines. (2) Assess each line's effectiveness and select the optimal one (shown in red). (3) Based on the best linear split-line, generate nonlinear alternatives by: (3.1) rotating the polygon, and (3.2) creating a grid of spline control points. (4) Generate and assess multiple nonlinear split-lines. (5) Identify the final split-line. (6) Perform the split and iterate the process. Reproduced with permission from Daumantas and Spiridonov (2024b).

When using *hespdiv*, the user must decide which type of boundaries to employ. This is specified using the logical argument *c.splits* (i.e. "curved split-lines?"). Regardless of the chosen option, *hespdiv* first identifies the most optimal straight line. If linear boundaries are selected, this line is used directly for subdivision. If nonlinear boundaries are selected, the straight line serves as a starting point for constructing the spline-based nonlinear boundaries (see Fig. 25 step 3).

To construct linear split-lines, *hespdiv* places a specified number of split-points at regular intervals along the perimeter of the polygon bounding the data (Fig. 25 step 1). Initially, this polygon is either the convex hull of the data points or a user-supplied study area polygon. In subsequent steps, it refers to one of the polygons produced by earlier subdivisions. The number of placed points is controlled by the argument *n.split.pts*. The default value is relatively low (16), which is appropriate for rapid exploratory runs, as higher values carry a substantial computational burden.

Once the split-points are placed, they are connected to form straight split-lines—candidate boundaries that divide the data and bounding polygon into two parts. In total, $\frac{n(n-1)}{2}$ split-lines are constructed. However, some may intersect the polygon perimeter or run along it. Such split-lines are identified and removed. As a result, the actual number of valid split-lines is often lower than the theoretical maximum, depending on the geometric complexity of the bounding polygon (with more complex geometries yielding a higher rate of discarded lines).

Nonlinear boundaries in *hespdiv* are constructed as mathematical splines, using the optimal linear boundary as a starting point (Fig. 25 step 3). The coordinate system is first rotated so that the linear boundary becomes horizontally aligned, with its left end positioned at the origin (Fig. 25 step 3.1). This simplification facilitates subsequent computations. A user-defined number of vertical columns of spline knots (*c.X.knots*, default = 5) are then regularly distributed along the horizontal axis, perpendicular to the original linear split-line (Fig. 25 step 3.2). Each column contains a specified number of knots (*c.Y.knots*, default = 10), distributed evenly across the vertical extent of the rotated polygon.

The algorithm proceeds by cycling through each column of knots, using different combinations of knots to construct candidate nonlinear split-lines via spline interpolation (see Fig. 25 step 4), testing their performance. Thus, optimisation directs the construction of nonlinear split-lines. Initially, the algorithm assumes that the best combination of knots lies directly on the linear split-line. If adjusting the knots results in a more optimal subdivision, this combination is updated. Two optimisation algorithms are available, selected via the logical argument *c.fast.optim*. These algorithms differ in the timing at which updates are applied.

Under the default algorithm (i.e. when the argument is set to FALSE), the update is applied only after a complete pass through all knot columns and all possible modifications have been tested. This update introduces a single change to the currently best-performing knot combination. The process is then repeated iteratively until no further improvements can be identified. The alternative is a greedy optimisation strategy, which updates the best knot combination immediately upon encountering a superior configuration. As a result, multiple updates to the best knot combination may be made within a single pass through the knot columns. Like the default algorithm, it terminates once no further enhancements are found following a full iteration. Thus, the selected optimisation strategy influences the nature of the nonlinear split-lines that are constructed and tested.

Boundary testing

The subdivision method determines how the constructed boundaries (split-lines) are tested. Irrespective of whether a split-line is linear or nonlinear, its evaluation follows the same procedure, consisting of three main steps (Fig. 26):

1. The split-line is applied to divide the occurrence dataset and the corresponding polygon into two parts (Fig. 26A).
2. These resulting subsets are checked against specific subdivision criteria—such as minimum required sample size, polygon area, or number of unique locations—to determine whether the subdivision is valid (Fig. 26B).
3. The two subsets are then compared using a chosen subdivision method to calculate a numerical comparison value that represents the effectiveness of the split-line (Fig. 26C).

Subdivision criteria can be set in absolute terms or relative to the dataset being divided. By default, the relative criteria ensure that resulting polygons and data clusters are roughly comparable in geographical area, number of occurrences, and distinct locations, allowing a maximum disparity of 1:4. The only absolute criterion applied by default is that the smaller polygon must represent at least 5% of the entire study area. All these criteria can be modified via *hespdiv()* function arguments.

The subdivision method specifies how the two subsets are compared and determines how the resulting comparison value—and, by extension, the effectiveness of a split-line—should be interpreted. In hespdiv, this method can be implemented in a modular fashion through separate generalisation and comparison functions. The generalisation function first processes each data subset delimited by a boundary (see Fig. 26A); its outputs are then passed to the comparison function for evaluation. This modular architecture can greatly simplify the comparison function, improving readability and code economy when a complex generalisation step is required. The design is optional, however: all necessary operations, including generalisation, may instead be incorporated directly within a single comparison function.

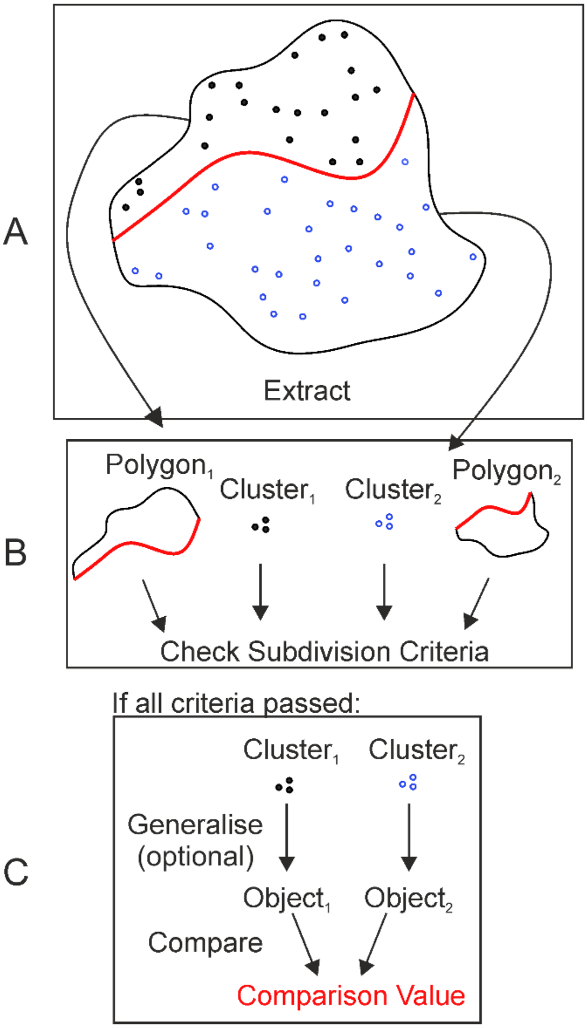


Figure 26. Visual representation of the three-step process for evaluating split-line performance: A – A split-line (red) divides the occurrence dataset and its polygon into two separate parts. B – The resulting subsets are checked to ensure they meet the required subdivision criteria. C – The subsets are then compared using a specific subdivision method by applying a combination of generalization and comparison functions to filtered datasets. Reproduced with permission from Daumantas and Spiridonov (2024b).

By default, this comparison method employs the Morisita–Horn similarity index (Horn, 1966), a simplified and computationally efficient variant of the original Morisita index (Morisita, 1959). This index measures how similar two species assemblages are, based on the overlap in their relative species occurrence frequencies. Unlike simpler indices like Sørensen or Jaccard, which only consider presence/absence information, the Morisita–Horn index incorporate frequency information and remains unaffected by differences in sample size or species diversity (Wolda, 1981). However, the latter two indices are also implemented within *hespdiv* and are available as alternative subdivision method choices. Morisita-Horn formula used is as follows:

$$C_{\hat{\lambda}} = \frac{2\sum_{i=1}^{S} x_i y_i}{\left(\sum_{i=1}^{S} x_i^2 + \sum_{i=1}^{S} y_i^2\right)\sum_{i=1}^{S} x_i \sum_{i=1}^{S} y_i}$$

Eq. 13

The Morisita–Horn similarity index, $C_{\hat{\lambda}}$, ranges from 0 (indicating no shared species composition) to 1 (indicating identical species proportions). For each species *i*, x_i and y_i represent the number of occurrences within HespDiv polygons *x* and *y*, respectively. S denotes the total number of species present across both polygons. This subdivision approach primarily relies on a list of species occurrences, although it can be adapted to work with abundance data. The values of x and y are obtained by calculating frequency tables from spatial subsets of the occurrence list.

Other subdivision methods are described in the documentation of the “hespdiv” package, specifically within the help file for the main function hespdiv(). Alternatively, hespdiv allows users to implement bespoke subdivision methods by supplying their own comparison and, if required, generalisation functions. In such cases, the logical argument *maximize* must also be specified to indicate how the output of the comparison function should be interpreted and optimised. Setting *maximize = TRUE*, for example, instructs the algorithm that higher comparison values represent better partitions. Altering the subdivision criteria—such as setting a minimum post-subdivision polygon area expressed as a proportion of the parent polygon—can also substantially change the output, even when the comparison function remains the same. These criteria, however, do not determine the subdivision method in the same way that the comparison and generalisation functions do; rather, they represent alternative subdivision strategies—for example, halving or decimating areas, occurrence counts, or numbers of localities.

Output and its Analysis: “hespdiv” package infrastructure

The hespdiv() function returns an object of class hespdiv (an R list) that contains comprehensive information on the resulting spatial subdivisions, including split-lines, HespDiv clusters, polygons, and the original function call. Summary statistics are organised in two data frames—'split.stats' and ‘poly.stats’.

The “hespdiv” R package (Daumantas, 2024) also supplies a suite of tools for post-processing, validation, and visualisation (see Appendix S2 in Daumantas & Spiridonov, 2024). Notably, the cross_comp() function enables cross-comparison of all generated HespDiv clusters, using the same comparison function specified in the original hespdiv() call. The output is a comparison matrix that can be explored further with clustering or network-based techniques.

Beyond standard map displays that show the hierarchical subdivisions and split-line performance, the package offers advanced visualisation options. These include an interactive 3-D representation in which each HespDiv polygon is extruded to a height proportional to any chosen statistic (e.g. the mean or standard deviation of the comparison values for all split-lines tested within that polygon). In this view, polygons appear as stacked blocks, overlaid by the blocks of their descendant polygons, forming intricate arrangements of pyramids, towers, and platforms. Such structures can reveal patterns and relationships that are difficult to discern from tabular output alone.

To evaluate the reliability of the split-lines, users may conduct either null-hypothesis testing or sensitivity analysis.

Null-hypothesis testing:

The function nulltest() implements a permutation-based procedure to assess the statistical significance of each split-line. Species-occurrence data are randomly permuted many times, thereby removing any spatial structure. Split-line comparison values are recalculated for every permutation, producing an empirical distribution under the null hypothesis of no spatial pattern. The output includes (i) a boxplot comparing the observed split-line performance with the null distribution and (ii) quantiles of the observed comparison values.

Sensitivity analysis:

Sensitivity analysis involves re-running the hespdiv() algorithm with alternative parameter settings—for example, using different subsamples of the original data—to observe how the resulting subdivisions change. This approach helps visualise alternative partitioning schemes and gauge how consistently HespDiv polygons are recovered under varying conditions. It also addresses cluster stability, which is especially important when data are sparse or unevenly distributed; in such cases, markedly different polygons may nonetheless capture similar sets of occurrences.

Cluster stability is quantified by measuring the overlap between the original clusters and their closest counterparts in each alternative subdivision. These counterparts are obtained by applying the new polygons to filter the same occurrence data used in the initial run. The Jaccard similarity index is then used to quantify overlap, representing the proportion of shared occurrences relative to the total number of occurrences. Closest counterpart cluster is the one with the highest Jaccard similarity index and the value of index reflect how similar the clusters are.

Since the original publication of *hespdiv* method (Daumantas & Spiridonov, 2024b), the associated R package has been significantly expanded, incorporating additional features for split-line significance testing, visualisation, and sensitivity analysis. These updates are currently available within the “newfeatures” branch of the “hespdiv” package GitHub repository. The latest package version, including all recent enhancements, can be installed in R (version >= 4.0) (after installing RTools—a toolchain required to build R packages from source on Windows) with the following commands:

```
if (!require("devtools")) install.packages("devtools")
devtools::install_github("Liudas-Dau/hespdiv", ref = "newfeatures")
```

The recent updates include: (1) a dendrogram option to visualise subdivision results; (2) a non-recursive sensitivity analysis function, which explores alternative subdivisions within individual polygons, in contrast to the original recursive sensitivity analysis that illustrated how the entire subdivision structure varied with parameter choices; (3) a function for generating rotating GIF animations of the 3D polygon visualisations; (4) an additional colour-coding option in the main visualisation function, allowing split-lines to be colour-coded by their hierarchical ranks rather than by their performance; and (5) extended functionality and new functions that support detailed analyses of taxonomic contributions to split-line performance, identifying taxonomic groups that actively contribute to, remain neutral about, or negatively impact the subdivisions. This set of features remains actively under development, with further expansions planned. Given the scope of this thesis is to present a general methodological framework, these new features will be covered in forthcoming publications.

Overall, the ‘hespdiv’ R package provides a comprehensive infrastructure that supports multiple complementary approaches, offering a robust framework for assessing the validity and reliability of subdivision results, along with diverse visualisation options to address various research questions and interpretative needs.

3.2.2. *birese*

The *birese* (**bi**nary **re**cursive **se**gmentation) method operates similarly to the *hespdiv* method but is designed for one-dimensional data, which can be either spatial or temporal. Its primary aim is to recursively subdivide a spatial transect or time series into segments by optimising the outcome of a specified comparison function. Although this method has not yet been formally proposed, it has been successfully applied in a published case study concerning the estimation of the duration of the *Mulde/lundgreni* biotic event using ostracod data (see Rinkevičiūtė et al., 2025). In that publication, the method was not yet named *birese* but was instead referred to by its full descriptive name. The algorithm and corresponding R code were presented in the supplementary materials accompanying that paper. However, the method has not yet been incorporated into the "hespdiv" R package. Consequently, the *birese* method is currently less functionally complete than *hespdiv*, although it is sufficiently robust to yield key research findings.

The *birese* method follows the same three-step procedure as *hespdiv*:

1. Construct a set of candidate boundaries that partition the spatial transect or time series into two segments.
2. Evaluate each candidate boundary using a predefined comparison function, and select the optimal boundary to establish the subdivision.
3. Repeat steps 1 and 2 recursively for each newly created segment until the specified stopping criterion is satisfied.

Despite their similarities in the general algorithmic workflow, the *birese* and *hespdiv* methods differ significantly in their implementation details. The *birese* method places boundaries—referred to as split-points—at midpoints between consecutive samples along the transect. This represents an advancement over *hespdiv*, as such split-point placement results in all possible unique binary partitions of the transect being evaluated.

Once boundaries have been defined, they are assessed similarly to *hespdiv*, although *birese* lacks the modular design of subdivision methods present in *hespdiv*. In *birese*, the subdivision method is defined entirely by a single comparison function, meaning any necessary generalisation steps must be incorporated directly into this function. Specifically, the evaluation process involves:

1. filtering data points on either side of each split-point;
2. verifying that the resulting segments meet a predefined minimum sample size criterion (set by *min.bucket* argument);
3. calculating the comparison value for the split-point using the specified comparison function.

The stopping criterion in *birese* is based on the minimum number of samples required in a resulting segment for a subdivision to be attempted (it set by *minsplit* argument, default is 2 x *min.bucket*).

The *birese* function produces two main outputs as R lists: one containing a data frame detailing the ranges of segments, partition locations, comparison values, and hierarchical information; the other containing individual data frames that plot comparison values against partition locations for each segment. An additional R function was developed specifically for visualisation of these results. This function generates rectangles representing each segment, with rectangle heights reflecting the comparison values associated with each partition. Additionally, it places a vertical line within each partitioned segment at the exact position of the split-point used for the partition. Lower-order segment rectangles are overlaid by higher-order segment rectangles, resulting in distinct visual patterns resembling pyramids, towers, stepped valleys, platforms or other structures. These visual structures provide crucial insights and facilitate interpretation, as demonstrated in the accompanying case study (Rinkevičiūtė et al., 2025).

3.3. Case Studies

Before discussing HespDiv methods and comparing them with alternative approaches it is worth exploring their applications.

3.3.1. Biogeography of Miocene Mammals

The *hespdiv* method was applied in a case study to uncover biogeographical patterns among Miocene mammals across the contiguous United States (Daumantas & Spiridonov, 2024b). The primary aim of the study was to illustrate and assess the method's performance. In short, the method revealed hierarchical biogeographical patterns that in many ways are supported by previous research and aligns with geographical barriers which grants some credibility.

Data

The selection of the study area, time interval, and taxonomic focus was driven by practical considerations, particularly the availability of fossil occurrence data and the existence of a well-established biogeographical framework for comparison (Tedford et al., 2004; Tedford et al., 1987). The Miocene epoch, spanning approximately 18 million years (23.03–5.33 Ma), witnessed several major climatic shifts that influenced faunal compositions across multiple spatial scales (Steinthorsdottir et al., 2021). At first glance, this temporal frame may appear too broad for bioregionalisation, especially given that the average species lifespan during the Miocene was around one million years (Žliobaitė & Fortelius, 2022). Consequently, the selected interval encompasses diachronic species assemblages composed of roughly 18 "half-generations" of species. However, subdividing the Miocene into narrower temporal bins would have substantially reduced both the number and spatial distribution of available fossil occurrences. Moreover, under the Bretskyan hierarchy framework, the units of the International Chronostratigraphic Chart represent global Bretskyan hierarchy entities, or distinct instances of Gaia (Spiridonov & Eldredge, 2024). The Miocene, as one such unit, defines the unifying global context to which the fossil dataset belongs. Considering the diachronic nature of the dataset, the bioregions identified in this case study can be interpreted as zones of dynamic compositional stability—structures shaped by the distributional patterns of successive species generations responding to long-term environmental and climatic fluctuations.

Flying and marine mammals were excluded from this study due to their differing dispersal capacities and their association with distinct environments, respectively. The fossil occurrence dataset was downloaded from the Paleobiology Database (https://paleobiodb.org/) on 12 April 2023, using the following parameters: base_name = Mammalia, idreso = species, idqual = certain, cc = US, state != Alaska, interval = Miocene, timerule = major, taxon_status = all, pres = regular, show = full, genus, strat, timebins, timecompare, ref, crmod. The initial download included 6112 occurrences (Daumantas & Spiridonov, 2024a). This dataset reflects typical characteristics of palaeontological occurrence data, such as uneven spatial distribution, incomplete coverage, and highly variable observation counts per site (ranging from 1 to over 500). Such variability exemplifies the multiscale, multifractal spatial patterns often seen in the fossil record (Plotnick, 2017).

Subsequently, records were filtered to exclude marine mammals (cetaceans and pinnipeds), flying mammals (Chiroptera), and terrestrial mammals that: (1) lacked coordinates, (2) had coordinates with errors greater than 1°, or (3) fell outside the modern borders of the contiguous United States. After filtering, 5244 occurrences remained (Daumantas & Spiridonov, 2024a). Most occurrences are concentrated in the western and central parts of the United States. The most abundant families in the dataset are Equidae (1060 occurrences) and Canidae (964 occurrences), with notable contributions from Rhinocerotidae (448), Merycoidodontidae (388), Heteromyidae (285), and Camelidae (255).

Three variables from this dataset were used in the study: *accepted_name* (species names), *lng* (longitude), and *lat* (latitude). Longitude and latitude were compiled into a data frame named *sp.coords*, while species names were stored in an R vector named *species*. Additionally, a data frame named *us*, containing the US border coordinates, was used; this was sourced from the *world* dataset in the "spData" R package (Bivand et al., 2022). All coordinates were based on the WGS84 system. The complete datasets, metadata, and processing scripts used in the study are available through the HDData R package, which can be installed by running devtools::install_github("Liudas-Dau/hespdiv_data") in R.

Parametrisation

The results were obtained by running this *hespdiv()* function call (Daumantas & Spiridonov, 2024a):

hespdiv(data = species, xy.dat = sp.coords, study.pol = us, n.split.pts = 75)

All parameters were left at their default settings, except those specifying the fossil occurrence data (data and xy.dat), the study area polygon (study.pol), and the number of perimeter split-points (n.split.pts).

To improve the fit of linear split-lines—and by extension, the derived nonlinear split-lines—the number of perimeter split-points was increased to 75, exceeding the default (15) at the cost of computation speed.

Finally, to assess the robustness of the results, a sensitivity analysis was conducted by executing 100 repeated runs of hespdiv, each using a random 80% subset of the fossil occurrence dataset.

Results

In total, *hespdiv* identified 28 HespDiv clusters and polygons by establishing 14 split-lines (Fig. 27). The clearest spatial representation of these polygons is provided by the blok3d() function, which visualises higher-order polygons stacked atop lower-order ones.

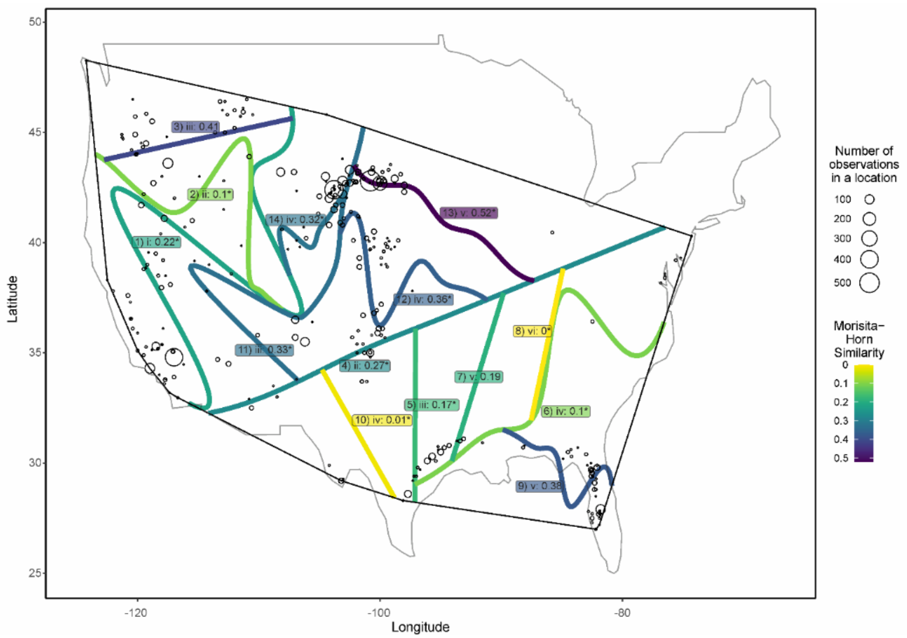


Figure 27. The map generated by applying the plot_hespdiv() function to the results. It illustrates the hierarchical subdivisions derived from the US Miocene mammalian assemblage data. Each split-line is labelled with its identification number (indicating the sequence in which it was derived), its hierarchical rank (denoted in Roman numerals), and the Morisita–Horn similarity value, which is also represented by colour. Statistically significant split-lines are marked with an asterisk. The size of each circle on the map corresponds to the number of taxa recorded at that fossil locality. Reproduced with permission from Daumantas and Spiridonov (2024b).

Split-line significance testing was conducted using the permutation-based nulltest() function, which involved shuffling the occurrence dataset 500 times and re-evaluating split-line performance. This Monte Carlo test revealed that all split-lines—except the 3rd, 7th, and 9th—were statistically significant (Fig. 28).

The split-lines located within the interior of the United States exhibited the lowest performance. Most split-lines were oriented longitudinally or diagonally, with strictly latitudinal orientations being rare. The United States was subdivided into three principal bioregions of comparable size: (1) the West Coast and Northwest, delineated by the 1st split-line; (2) the Central Plains; and (3) the Southeast—both distinguished through a subsequent subdivision with the 4th split-line.

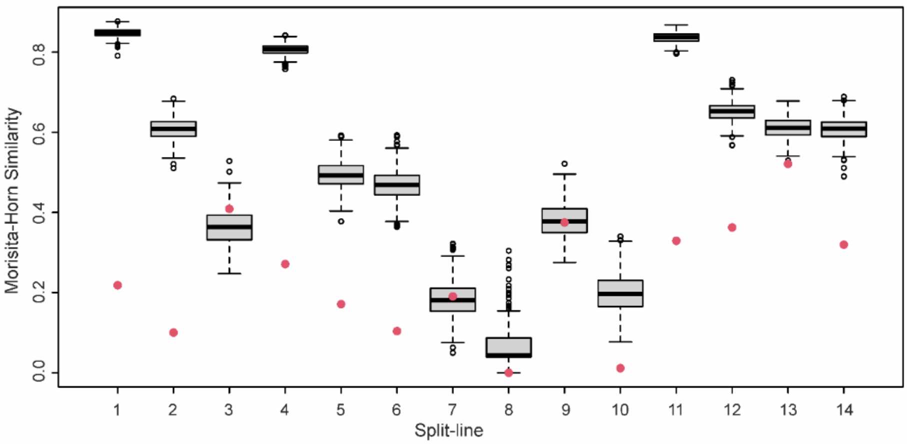


Figure 28. Statistical significance of split-lines assessed using the nulltest() function. Red dots represent the original empirical performance of each split-line, while the boxplots illustrate the distribution of performance values generated from 500 randomised reshufflings of the occurrences. Reproduced with permission from Daumantas and Spiridonov (2024b).

A cross-comparison matrix of the resulting HespDiv clusters was analysed using hierarchical clustering. The dendrogram supported this spatial structuring: clusters A, B, and C in Fig. 29 correspond to the aforementioned West Coast and Northwest, Central Plains, and Southeast bioregions, respectively. The only deviation was the assignment of the B.1 subcluster (part of Southeast) to cluster B (Central Plains) rather than to cluster C (Southeast). Smaller subclusters also reflected relationships evident in the original *hespdiv* results. For example, clusters C.1 and C.2 in Fig. 29 correspond to bioregions produced by the 6th split-line; similarly, the two very different subclusters within cluster A (West Coast) align with bioregions produced by the 2nd split-line, which also indicated considerably lower similarity (0.1 Morisita-Horn similarity) between the two bioregions.

Geographical proximity appears to explain much of the similarity between clusters observed in the dendrogram, as does the size of the corresponding regions, and the spatial overlap of geographically nested bioregions (e.g. note the grouping of bioregions 9 and 8, and the clustering of bioregions 6 and 2). The Central Plains bioregion (cluster 21) appears to serve as a good representation of the entire Miocene fossil mammal dataset for the US, as it is comprised of relatively small dataset but was grouped in the same subcluster as cluster 1, which corresponds to the complete dataset.

The sensitivity analysis performed with *hespdiv* provided insights into the stability of the identified HespDiv clusters and polygons. When all alternative subdivisions were displayed on a single map (Fig. 30 A), the resulting visual impression was that polygon boundaries are generally unstable, and that the originally identified subdivision (Fig. 27) was only weakly represented among the alternatives.

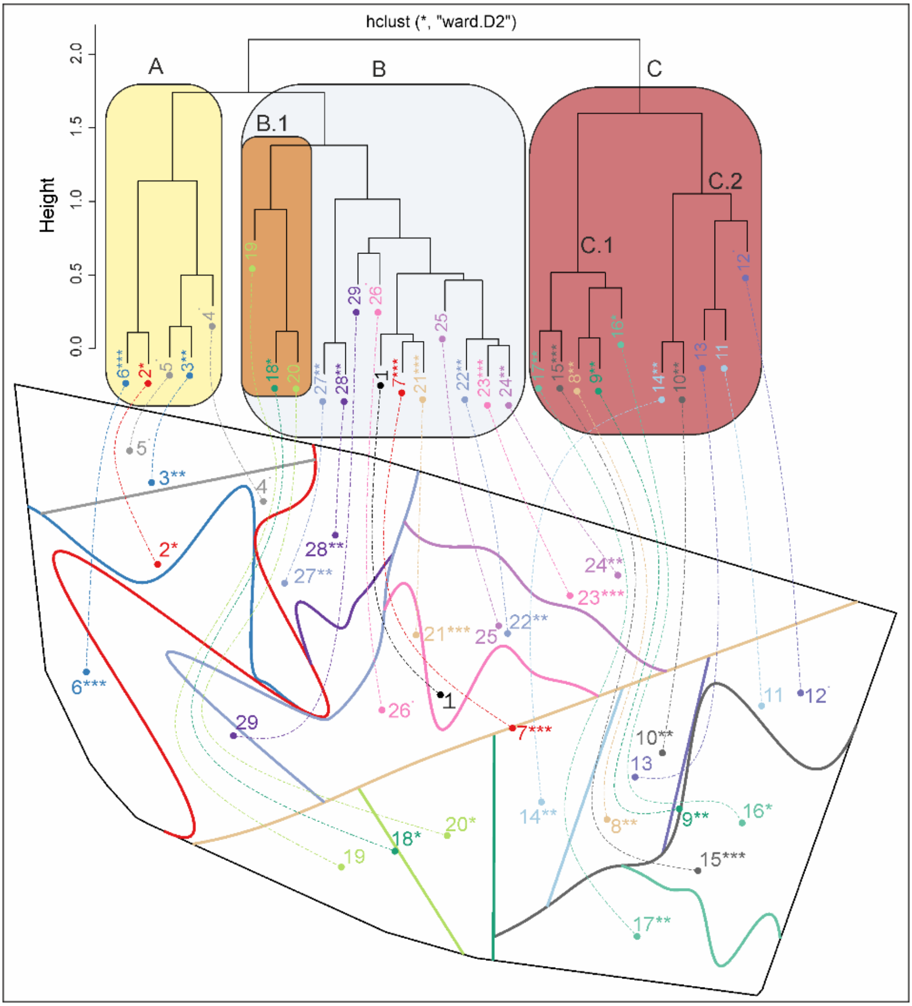


Figure. 29. Relationships among HespDiv polygons illustrated through a cluster dendrogram. The lower section of the figure shows the HespDiv polygons, visualised using the poly_scheme() function, while the upper dendrogram was generated by applying hierarchical cluster analysis to a distance matrix derived from the output of the cross_comp() function. Each polygon is represented by its centroid, label, and the colour of the split-line that generated it. Cluster stability, as determined through sensitivity analysis, is categorised into five levels and indicated using asterisks or a dot: *** very stable—more than 95% of alternative subdivisions produced a closely matching 'analogue' cluster (with Jaccard similarity ≥ 0.75); ** stable—at

least 50% produced a similar analogue cluster; * mostly stable—at least 25% produced a similar analogue cluster, with no more than 25% producing a dissimilar one (Jaccard similarity ≤ 0.25); • somewhat stable—at least 25% produced a similar analogue cluster, while between 25–75% produced dissimilar clusters, or no more than 25% produced dissimilar clusters. Polygon identification numbers reflect the sequence in which they were derived, with Polygon 1 representing the entire study area. Reproduced with permission from Daumantas and Spiridonov (2024b).

Alternative subdivision split-lines showed strong convergence in regions with high fossil occurrence density, while they varied considerably in fossil-poor regions. In some cases, where split-lines intersected an isolated fossil-rich locality within a surrounding fossil-free area, a clear convergence of split-lines was observed at that locality, with split-lines radiating outward from that locality as if they were rotating around it (e.g. note the split-lines in Fig. 30 C corresponding to the 4th split-line in Fig. 27).

In maps showing alternative subdivisions of different hierarchical ranks, the established split-lines up to the second order (e.g. 4, 2, 1) were clearly discernible, whereas third- to fifth-order split-lines were only partially represented (compare Fig. 27 with Fig. 30B-F) Interestingly, the first established split-line—which is the most important hierarchically—showed several possible alternatives (Fig. 30 B), most of which were oriented southeast–northwest. One alternative was a linear variant of the established curvilinear split-line.

Some higher-order alternative split-lines also showed localised convergence zones, although no convergence was observed for split-lines at the 6th or 7th rank (compare Fig. 27 with Fig. 30G-H).

The sensitivity analysis of HespDiv clusters revealed that the majority (19) were stable, classified as either mostly stable, stable or very stable (Fig. 31). Only five clusters (29, 25, 19, 13, 11) were deemed unstable, while four clusters (26, 12, 5, 4) were considered somewhat stable. The unstable clusters were primarily further undivided high-order bioregions (clusters 4, 5, 12, 13, 19, 25, 26, 29), created either by statistically insignificant split-lines (e.g. clusters 4, 5, 11) or by the subdivision of already unstable clusters (e.g. clusters 12, 13).

A positive correlation was observed between the number of split-lines tested within a given HespDiv polygon and the performance of the split-line established there (Fig. 32). Polygons with more tested split-lines were associated with consistently lower and less variable Morisita–Horn similarity index values. In contrast, fewer split-lines were typically tested in higher-rank subdivisions, which were also more frequently associated with statistically insignificant split-lines

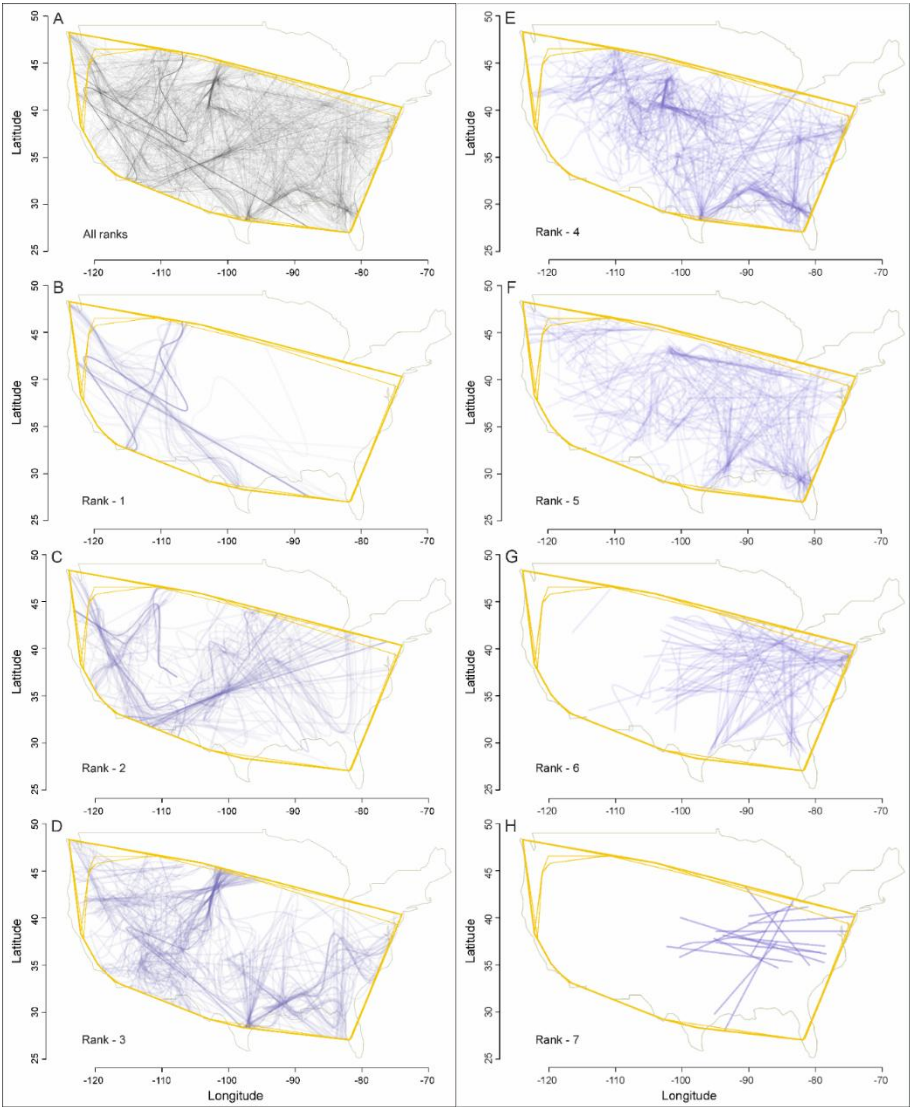


Figure 30. Stability of HespDiv polygons illustrated by plotting split-lines from all alternative subdivisions produced in the *hespdiv* sensitivity analysis. The plots were generated using the plot_hsa() function. Panel A shows all ranks combined, while panels B to H display split-lines ranked from 1 to 7, respectively. Reproduced with permission from Daumantas and Spiridonov (2024b).

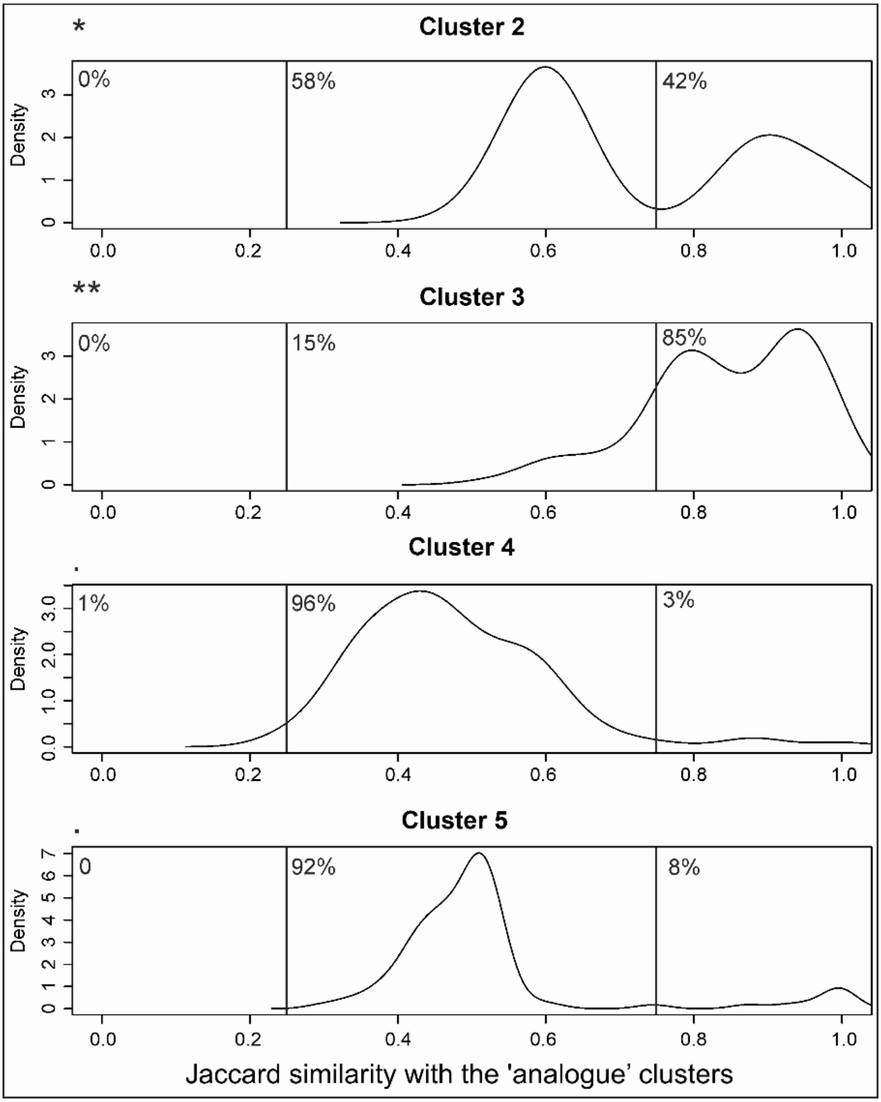


Figure 31. Stability of the 2nd to 5th HespDiv clusters illustrated by plotting empirical probability density functions (PDFs) of Jaccard similarity between the occurrences of established clusters and their most similar ‘analogue’ clusters identified in alternative subdivisions during the sensitivity analysis. Asterisks and dots indicate levels of HespDiv cluster stability: ** stable; * mostly stable; • somewhat stable (see Fig. 29 for definitions). Plots were generated using the plot_hsa_q() function. Stability results for clusters 6 to 29 are presented on the following two pages (figure continued). Reproduced with permission from Daumantas and Spiridonov (2024b).

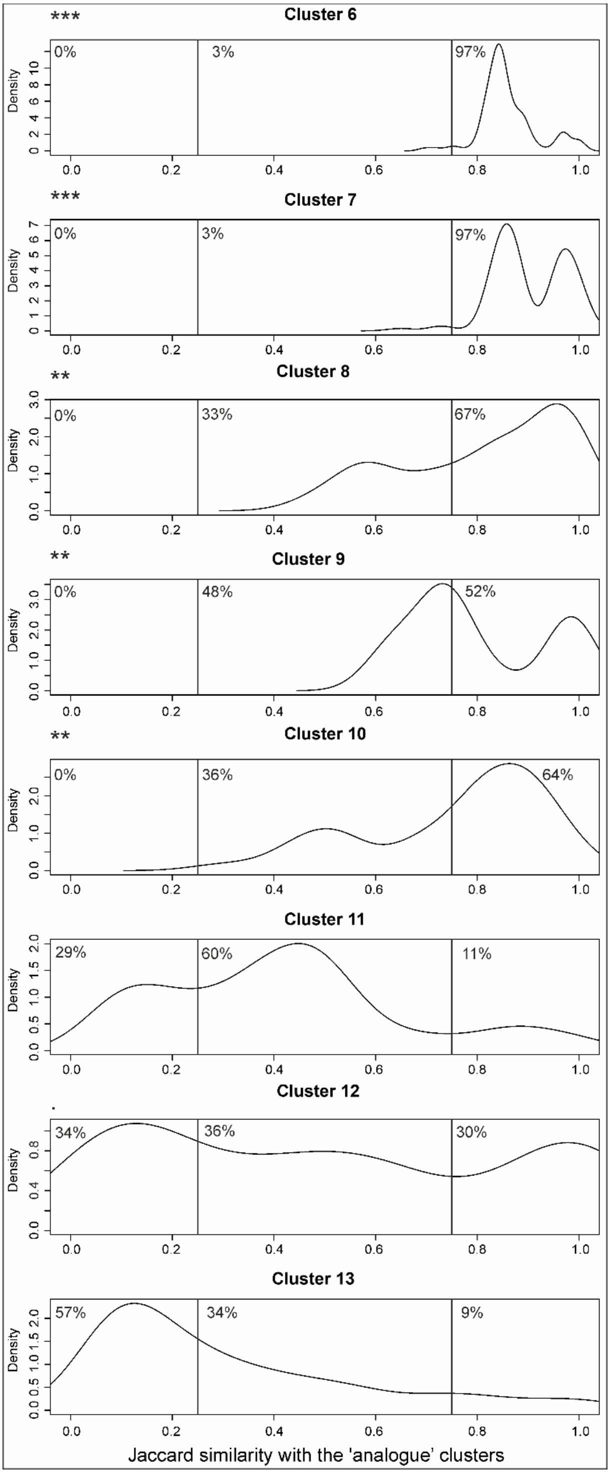


Figure 31. Continued.

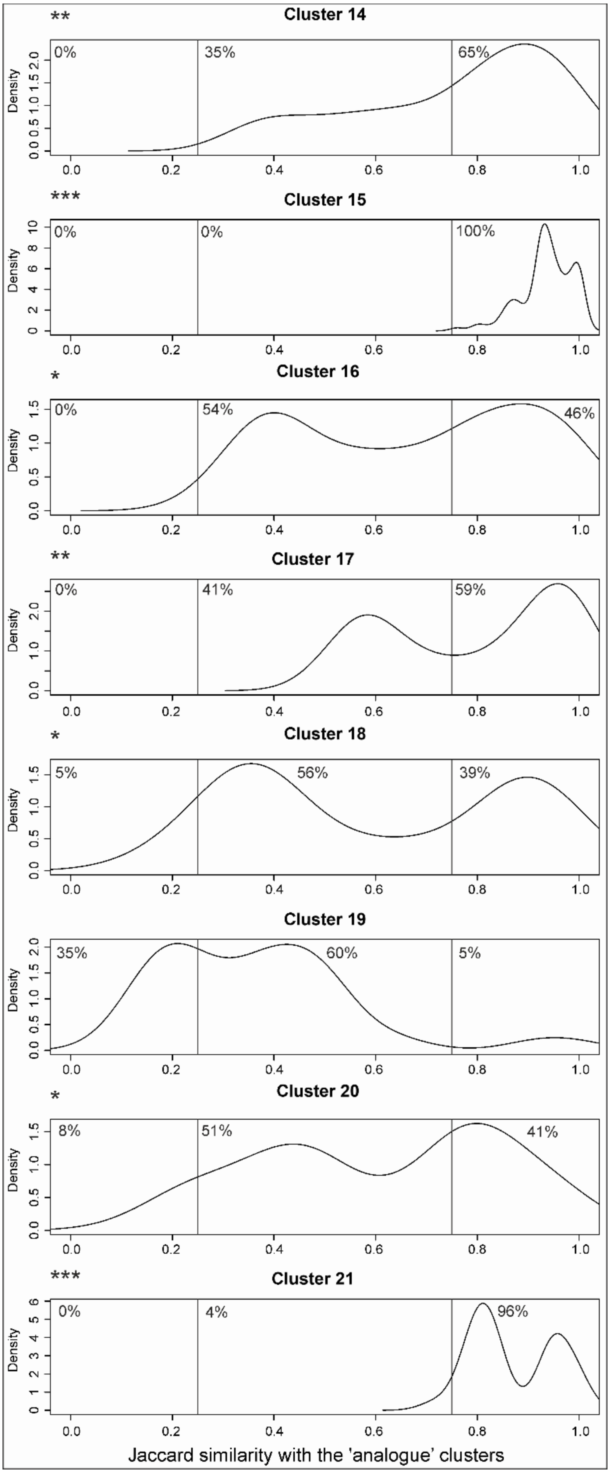


Figure 31. Continued.

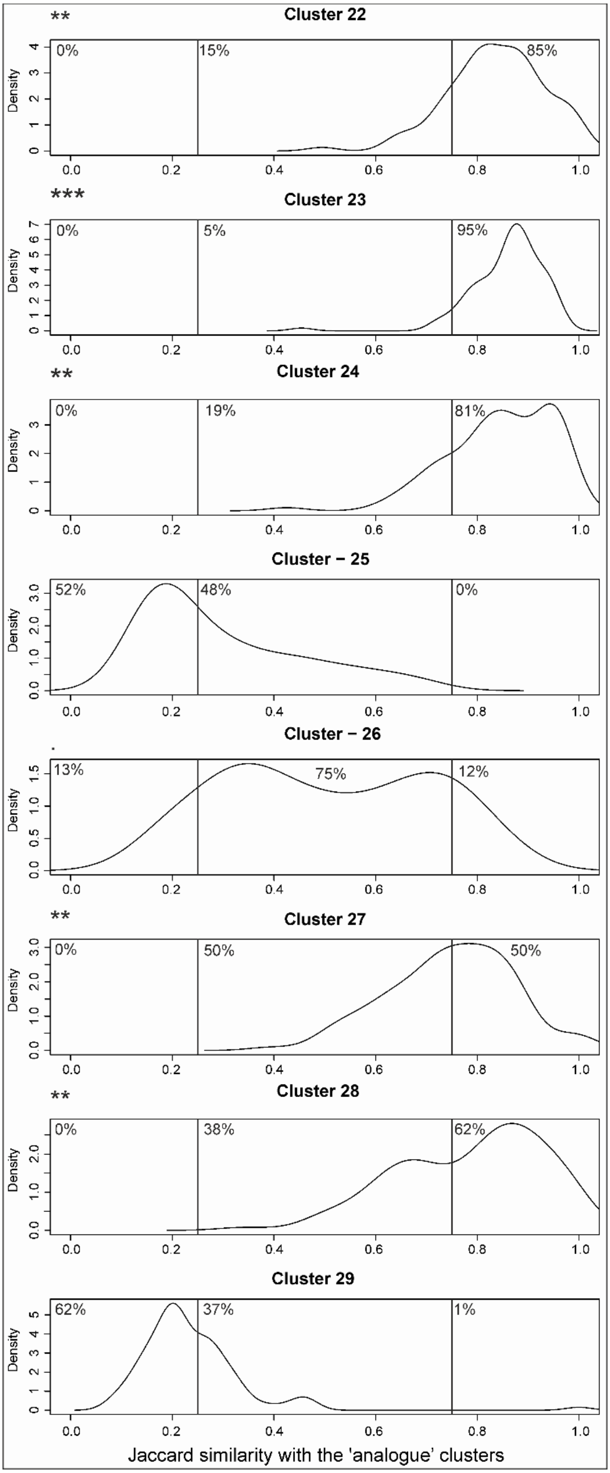


Figure 31. Continued.

The number of split-lines that can be tested is influenced by the polygon shape, size, and fossil occurrence density and distribution within the polygon. Large polygons with simple geometries and a high number of spatially well-distributed fossil occurrences tend to yield a greater number of viable split-lines and, consequently, a higher likelihood of producing high-quality, statistically significant subdivisions.

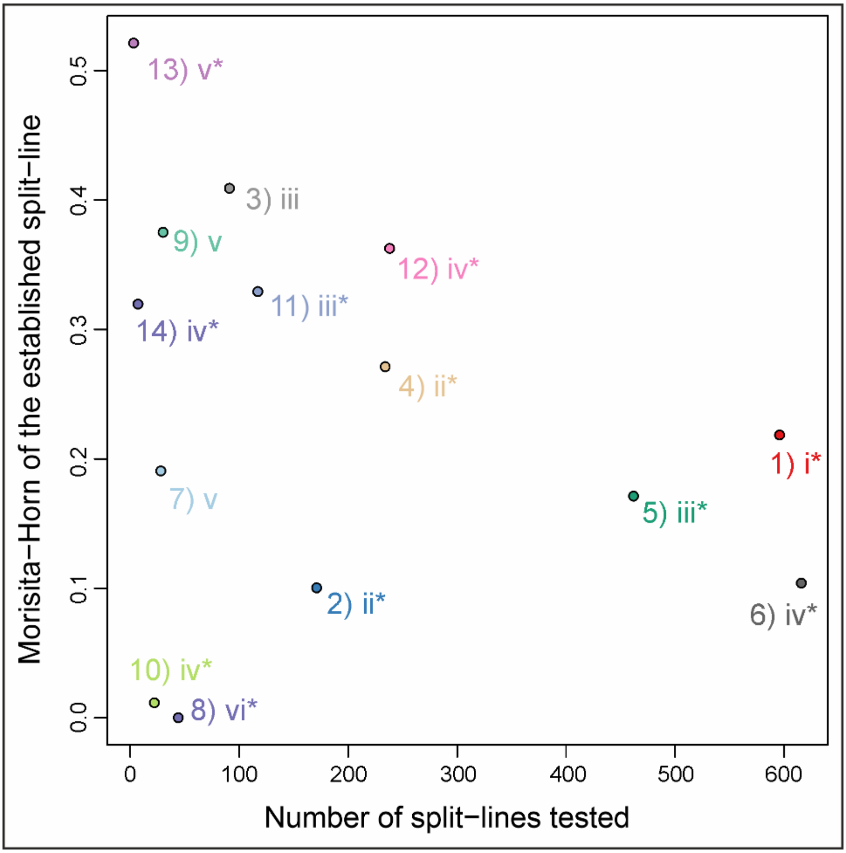


Figure 32. Relationship between the number of linear split-lines tested and the rank, comparison score, and statistical significance of the selected split-line. As in Fig. 27, each split-line is labelled with its identification number, rank (in Roman numerals), and an asterisk indicating statistical significance; colours correspond to those used in Fig. 29. Reproduced with permission from Daumantas and Spiridonov (2024b).

Discussion

The findings indicate a clear directional pattern in biogeographic structuring. Despite the sensitivity analysis showing some variability in the positioning of polygon boundaries, most of the identified split-lines followed either a diagonal or longitudinal orientation. This pattern suggests that latitudinal climate gradients alone are insufficient to explain the observed bioregional arrangement. Typically, stronger latitudinal turnover in species composition is associated with sharper latitudinal gradients in temperature and precipitation, while longitudinal turnover tends to dominate under more uniform climatic conditions across latitudes. During the Miocene—a time marked by moderate warmth—latitudinal climate gradients were relatively mild (Steinthorsdottir et al., 2021; Utescher et al., 2011). Using a distinct methodology, Gibert et al. (2022) also observed that the principal division of Miocene mammalian fossil assemblages in Europe aligned longitudinally. A similar, albeit secondary, longitudinal structuring was noted in Asia, persisting into the Pleistocene, whereas such patterns were absent in Africa. These findings suggest that longitudinal or diagonal structuring may be a general feature of Miocene mammalian faunas at mid to high northern latitudes. The absence of clear latitudinal partitions might also be influenced by large-scale landscape features and longitudinally or diagonally aligned physical barriers—such as coastlines, the Rio Grande Rift, and the Appalachian Mountains—that can shape biodiversity patterns (Fortelius et al., 2016; Perrigo et al., 2020). The role of topography is likely most pronounced in the first split-line, which follows a complex and highly irregular path intersecting notable Miocene regions such as the Basin and Range Province, the Rocky Mountains, and at those times volcanically active zones in the Northwest. This initial split-line also corresponds closely with boundaries demarcating wet and dry geofloras (see Shotwell 1961, Fig. 7), which were found to significantly influence horse biogeography (Shotwell, 1961). Therefore, the configuration and orientation of the split-lines are likely shaped by an interplay between climatic conditions and topographic features.

The performance of individual split-lines appears to follow a certain spatial pattern. Those located in the central United States—specifically between the 1st and 4th split-lines—tend to perform less effectively, which may reflect the lack of significant geographical barriers in that region, permitting greater faunal mixing. Similarly, the 3rd and 9th split-lines, which did not reach statistical significance, also show relatively weak performance. In contrast, split-lines that yield higher performance are frequently situated near coastal areas (e.g., the 5th, 6th, and 2nd split-lines) or separate geographically distant occurrence clusters (such as the 7th, 8th, and 10th split-lines). According to the Bretskyan hierarchy, higher split-line performance is expected when clusters are more distant from each other and when substantial physical barriers exist between them.

Janis (1998) proposed a classical non-hierarchical division of Miocene mammal bioregions in the United States, identifying 9 distinct bioregions (see

Fig. 33), a number significantly lower than the 28 bioregions (or 15 end-nodes) identified by the hierarchical method *hespdiv*. Direct comparison between these two bioregionalization frameworks is challenging due to several factors: they rely on different fossil datasets, apply different methodological principles (hierarchical vs. non-hierarchical), and differ both in the number of regions and the placement of bioregional boundaries. Moreover, both classifications may be considered inherently uncertain or subjective, with multiple plausible alternatives. Janis (1998) recognized that various researchers have produced differing bioregional frameworks. In a similar vein, the sensitivity analysis of the *hespdiv* method revealed the presence of several equally viable subdivision alternatives. This supports the notion that large-scale bioregions may generally lack sharp boundaries and exhibit a fuzzy character (Spiridonov & Eldredge 2024), meaning that bioregional delineations should be viewed in probabilistic rather than absolute terms.

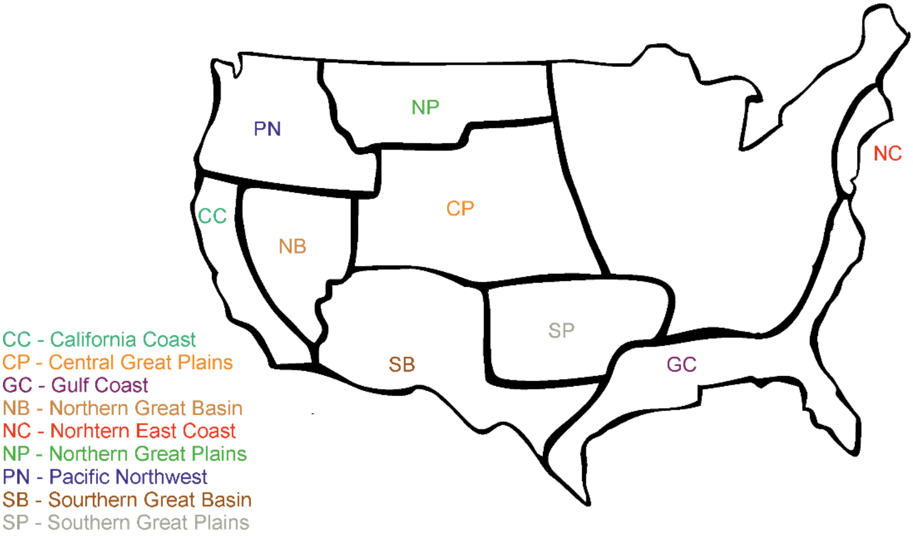


Figure 33. Bioregionalisation scheme of North American Tertiary mammals as proposed by Janis (1998), originally derived from Tedford et al. (1987). For easier comparison with Fig. 27, the map has been cropped to match the extent of the contiguous United States. Reproduced with permission from Daumantas and Spiridonov (2024b).

Despite these limitations, some overlap between the two schemes can be observed. The first split-line in *hespdiv* isolates a region (polygon 2) that roughly aligns with Janis' California Coast and Pacific Northwest bioregions. The second split-line further divides these areas. The Central Great Plains, Northern Great Basin, and parts of the Southern Great Basin appear to correspond to polygon 21 (Central Plains), while the remainder of the Southern Great Basin, along with the Southern Great Plains and Gulf Coast, aligns with polygon 7 (Southeast). Polygon 15 may represent the Gulf Coast more specifically. However, congruence between the two approaches diminishes at higher levels of subdivision. Notably, regions such as the Northern Great Plains and Northern East Coast were outside the spatial extent of the fossil dataset used in *hespdiv* and thus were not captured in its output. Both frameworks also notably lack subdivisions in the northeastern United States.

The three principal bioregions emerging from the *hespdiv* analysis—namely, the West Coast, Central Plains, and Southeast—show partial alignment with the bioregional framework proposed by Janis (1998). The second and twenty-first polygons, corresponding respectively to the West Coast and Central Plains and defined by the two highest-ranking split-lines, also broadly align with the West Coast and Midcontinent bioregions described by Alroy (1998) in his study on the diachronic patterns of mammalian first appearance events. Additionally, the four geographically distinct areas for the Equinae subfamily—Southwest, Great Plains, Gulf Coast, and Southeast—outlined by Maguire and Stigall (2008), show a degree of similarity to the three main bioregions detected by *hespdiv*. These parallels imply that the West Coast, Central Plains, and Southeast regions identified through *hespdiv* may represent genuine, large-scale Bretskyan units.

Conclusion

The *hespdiv* method appears capable of objectively detecting major biogeographic structures. This is supported by the fact form and effectiveness of its split-lines correspond well with recognized physical barriers. The three main Bretskyan-like entities detected (West Coast, Central Plains, and Southeast bioregions) also correspond relatively well to previous US Miocene mammal bioregionalization schemes. According to Bretskyan hierarchy framework, these bioregions can be classified as intracontinental geobiomes. Given the apparent robustness and ecological relevance of West Coast, Central Plains, and Southeast bioregions, their polygons could serve as practical territorial sampling units in future biogeographic investigations.

3.3.2 Duration and structure of Mulde/*lundgreni* event

Characterising the rates and stages of major extinction and faunal turnover events is essential for identifying the drivers of oceanic disturbances and for gaining insight into the processes and mechanisms underlying ecosystem transformations (Rinkevičiūtė et al., 2025). This case study aimed to characterise the rates and stages of the Mulde/*lundgreni* biotic event as revealed by ultra-high-resolution ostracod abundance data from the Gėluva-118 section. Referred to as the "Big Crisis" (Jaeger, 1991), the event was first identified through conodont and graptolite extinction records (Jeppsson et al., 1995; Jeppsson & Calner, 2002; Koren, 1991). Substantial evidence now suggests that the Mulde/*lundgreni* event had far-reaching global impacts on oceanic chemistry, circulation, climate, high amplitude sea-level variations, and stable oxygen and carbon isotope signatures (Jeppsson & Calner, 2002; Trotter et al., 2016). The event was likely triggered by the interference of the 4th and 5th Milankovitch cycles, resulting in the sea level regression (Radzevičius et al., 2017; Rinkevičiūtė et al., 2025; Andrej Spiridonov et al., 2017). Nevertheless, significant knowledge gaps remain regarding the event's timing, impacts, drivers, and underlying mechanisms, highlighting the relevance of this study.

This case study stands out due to its ultra-high-resolution sampling and the application of a quantitative approach to estimate the duration and tempo of the Mulde/*lundgreni* event. A previous high-resolution investigation of the event, based on ostracods from the Gėluva-118 core, involved sampling at approximately 0.8-metre intervals (Rinkevičiūtė et al., 2022). In contrast, the present study increased the resolution fourfold to 0.2-metre intervals at the focal interval around the *lundgreni* Event itself. From a methodological perspective, earlier studies provided only semi-quantitative estimates, suggesting that the Mulde/*lundgreni* event lasted approximately 1 million years (Cramer et al., 2012). In comparison, this study incorporates two novel approaches: the first application of the newly developed HespDiv method—*birese* (**bi**nary **re**cursive **se**gmentation)—and Bayesian geochronological age-depth modelling. The HespDiv method *birese* was employed at a critical stage of this investigation—namely, to establish the stages of the Mulde/*lundgren*i event and their stratigraphic boundaries. These outputs provided essential input for estimating the event's duration and characterising its distinct stages.

Geological Setting

The Gėluva-118 core is located in central-west Lithuania (55° 15′ 30.89″ N, 23° 23′ 24″ E). The palaeontological data sampled for this study derive from a core interval that encompasses much of the Middle and Upper Homerian (Wenlock, Silurian), with the exception of its uppermost part (Rinkevičiūtė et al., 2022). Based on graptolite data, the Jaagarahu and Gėluva regional stages have been identified within this interval (Rinkevičiūtė et al., 2022). The Riga Formation, assigned to the Jaagarahu stage, consists primarily of mudstones and packstones, with bentonite layers present in its lower portion. Similarly, the Gėluva Formation comprises mudstones and packstones, although bentonite interbeds occur only in its upper part (Rinkevičiūtė et al., 2022) (Fig. 34). The gradual variation in clay content is indicative of aggradational development within shelfal environment (Rinkevičiūtė et al., 2022). During the Late Wenlock and Ludlow, the site of the core would have been located on a shallow shelf along the southwestern margin of the Baltica palaeocontinent, within the eastern part of the Silurian Baltic Basin (Fig. 35). At that time, the Baltica continent was situated at low latitudes under predominantly equatorial conditions (Torsvik & Cocks, 2013), favourable to rich calcareous benthic paleofauna.

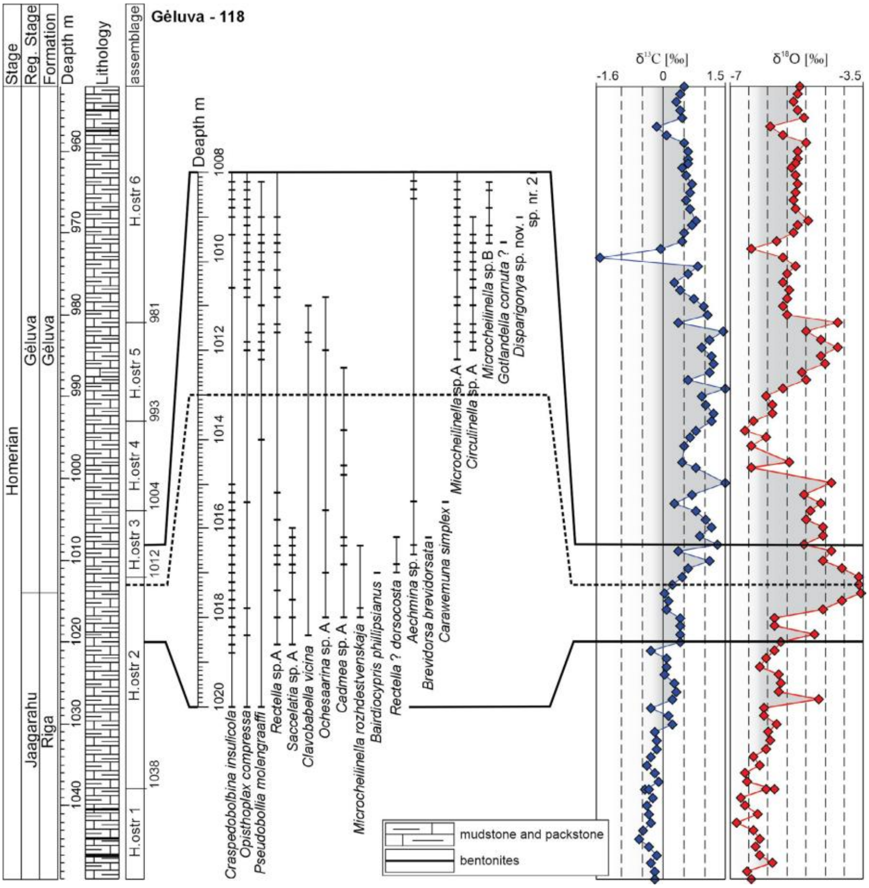


Figure. 34. The stratigraphic distribution of lithology, ostracod occurrences, and statistically significant (99% level) ostracod assemblage compositions is shown alongside carbonate δ13C and δ18O trends. Reproduced from Rinkevičiūtė et al. (2025), licensed under CC BY 4.0 (http://creativecommons.org/licenses/by/4.0/).

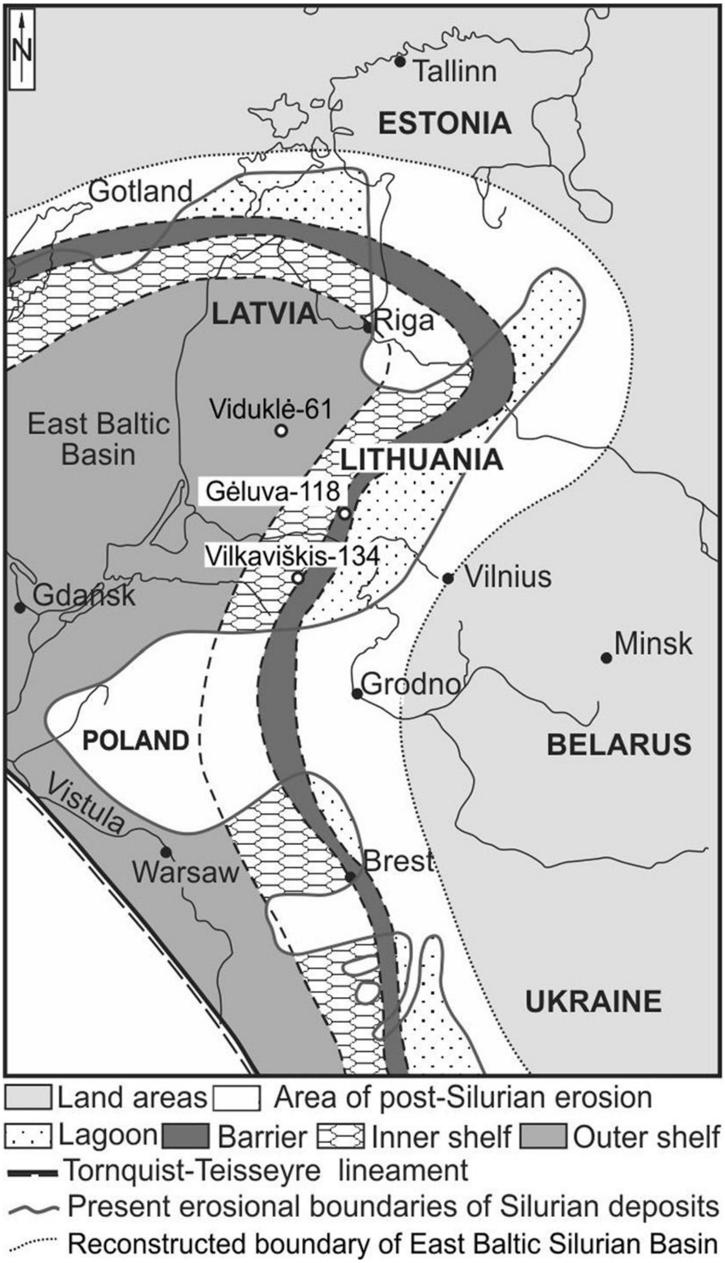


Figure 35. Location of the Gėluva-118 core and palaeogeographic reconstruction of the surrounding areas. The location of the Viduklė-61 core, which was important in establishing Gėluva-118 core geochronology via graphical correlation, is also shown. Map reproduced from Rinkevičiūtė et al. (2022).

Data

This study is based on (1) ultra-high-resolution ostracod abundance data collected from the Jaagarahu and Gėluva regional stages within the Gėluva-118 core, and (2) the established geochronological framework of the core.

Ostracod Abundance Dataset

Previous study based on ostracod, graptolite, d18O and d13C data collected between 952.1 m and 1049 m depth suggested approximate location of the Mulde/*lundgreni* event in the Gėluva-118 core (Rinkevičiūtė et al., 2022). In this study, 44 additional ostracod samples were taken every 20 cm from the event interval and its surroundings (1008 – 1018.8 m depth). Sampling and taxonomic analysis, as well as the ostracod abundance database creation was done by S. Rinkevičiūtė. The sampled interval corresponds to the *nassa* and upper *lundgreni* graptolite zones (Radzevičius, Spiridonov, & Brazauskas, 2014; Rinkevičiūtė et al., 2025). These new samples were integrated with the already published 97 ostracod samples (taken every 80 cm) from the previous study (Rinkevičiūtė et al., 2022). A total of 24587 ostracod observations of 31 distinct species were recorded in the combined ostracod abundance dataset. The bulk sample abundance varied greatly from 0 to 2876 ostracods per sample and was heavily skewed to large counts (average number of ostracods per sample 175.6, median 65). These characteristics made it essential to ensure that the selected methods for the study would be independent on sample size and diversity. The ostracod assemblage obtained in this study is curated at the Geological Museum of Vilnius University.

Gėluva-118 Geochronology

The geochronology of Gėluva-118 section was constructed by S. Radzevičius using chronostratigraphic markers identified via correlation with nearby core sections (Viduklė-61 and Šiupyliai-69). Key stratigraphic markers included: the Llandovery–Wenlock boundary (1120.5 m depth) defined lithostratigraphically (Paškevičius, 1997), the Grötlingbo Bentonite level (1012 m) projected from Viduklė-61 (Radzevičius & Paškevičius, 2000), the base of the Homerian stage (1059 m), and the Wenlock–Ludlow boundary (930 m). Graptolite and conodont biostratigraphy, lithostratigraphy, chemostratigraphy, and numerical cross-recurrence plot correlation were used as proxies for correlation and identification of stage boundaries between cores. Specific biostratigraphic markers included the first appearances of *Cyrtograptus murchisoni* (Wenlock base), *Cyrtograptus lundgreni* (Homerian base), *Gothograptus nassa* and *Pristiograptus parvus* (Gėluva Regional Stage base), *Neodiversograptus nilssoni* (Ludlow base), as well as the last appearances of *Monograptus flemingi* and *Pristiograptus pseudodubius*, alongside carbon isotopic excursions indicative of significant palaeoenvironmental shifts (Radzevičius & Paškevičius, 2000, 2005; Rinkevičiūtė et al., 2022; Spiridonov et al., 2020). This summary of the chronostratigraphic framework is based on Rinkevičiūtė et al. (2025), where the methodology is described in greater detail.

Methods

The methodology for this case study involved three steps: (1) distinguishing the stages of the Mulde/*lundgreni* event, (2) characterising these stages, and (3) evaluating their durations. The methodology is detailed extensively in the main paper and its supplementary materials (Rinkevičiūtė et al., 2025).

Distinguishing Mulde/lundgreni Event Stages

To characterise the stages and the progression rate of the Mulde/*lundgreni* event, these stages first needed to be distinguished within the core. The event was conceptualised as comprising three distinct stages:

- Collapse – initiation of environmental and ecological stress, marked by declining ostracod populations and diversity.
- Maximal Stress – characterised by the most extreme and hostile conditions, unsuitable for ostracods.
- Recovery – improvement of conditions, accompanied by the rebound of ostracod populations and diversity.

Although each stage could be identified individually, this study initially defined the Maximal Stress stage based on ostracod diversity and abundance metrics. Subsequently, the total Mulde/*lundgreni* event interval was delineated within the Gėluva-118 core using the *birese* method. The intervals immediately preceding and succeeding the Maximal Stress stage were then designated as the Collapse and Recovery stages, respectively. Additionally, intervals before and after the total Mulde/*lundgreni* event were classified as Pre-event and Post-event intervals.

To identify the Maximal Stress stage and characterise each event stage, the following metrics were employed: total sample abundance, species richness, the inverse Simpson index, and the Pielou evenness index. The Pielou evenness index varies between 0 and 1, reflecting the evenness of species representation within samples. As it is standardised by species count, it facilitates comparisons across palaeocommunities (Pielou, 1966). The Simpson index (D, (Simpson, 1949) represents the probability of drawing two individuals of the same species from a sample. Its inverse (1/D) reflects sample diversity and is very similar to Fisher's alpha ((Oksanen et al., 2022), see diversity() function in the "vegan" R package), which is a robust diversity index mostly independent from sample size (Buzas & Hayek, 2005; Spiridonov et al., 2021). However, unlike Fisher's alpha, the inverse Simpson index does not assume a specific rank-abundance distribution (Simpson, 1949). The total sample abundance served as a proxy for ostracod biomass. Prior to calculating these indices, ostracod taxonomic and abundance data were standardised by sample weight, reflecting ostracod counts per kilogram of rock.

The Morisita-Horn metric served as the comparison function within the *birese* method, chosen due to its robustness against variations in sample size and diversity (see Boundary Testing subsection in the hespdiv method description for details). The *birese* method required a minimum of 10 samples per segment for partitioning to be established (min.bucket = 10), and a minimum of 20 samples per segment to attempt a partition (minsplit = 20).

Characterising ostracod palaeocuminities

To characterise the ostracod palaeocommunities for each stage of the Mulde/*lundgreni* event, distributions of bootstrapped sample averages of diversity indices were visualised. Each bootstrap sample consisted of three samples, with a total of 1000 bootstrap samples drawn.

Evaluating Mulde/lundgreni event duration

To estimate the duration of the Mulde/*lundgreni* event and its constituent stages, a Bayesian age–depth model was developed using the established geochronology of the Gėluva-118 core. The model was constructed with the 'modifiedBChron' R package (v. 0.7.0; Trayler et al., 2020), an adaptation of Bchron (Haslett & Parnell, 2008) tailored for deep-time applications. Its independence from specific timescales is especially valuable, given the scaling behaviour of sedimentation rates (Kemp & Sadler, 2014). Stage durations were derived from the posterior distribution of sedimentation ages, while the Nyquist frequency was calculated to determine the minimum resolvable temporal fluctuations without incurring aliasing bias.

Results

A pronounced decrease in ostracod abundance, evenness, and species richness was observed in 14 consecutive samples between depths of 1015.1 m and 1012.3 m. Eight samples within this interval were barren, while the remaining samples contained only a single species, with a maximum abundance of 114 individuals per kilogram of rock. Consequently, this interval was designated as the Maximal Stress stage.

Segmentation of the Gėluva-118 section using the *birese* method revealed significant ostracod community shifts around the Maximal Stress interval (Fig. 36). All subsequent partitions within the segment spanning depths from 1016.3 m to 1009.1 m demonstrated notably greater community differences compared to the successive partitions identified in other segments. The Morisita-Horn values of the partitions within the interval were 0.10 and 0.01, whereas those of partitions outside the interval ranged from 0.55 to 1.00. Given that the Maximal Stress interval was encompassed entirely within this interval, the 1016.3 m – 1009.1 m interval was designated to represent the total extent of the Mulde/*lundgreni* event. Consequently, the interval from 1016.3 m to 1015.1 m was classified as the Collapse stage, and the interval from 1012.3 m to 1009.1 m as the Recovery stage. The Pre-Event interval was defined from the deepest samples (1049 m) to 1016.3 m, and the Post-Event interval extended from 1009.1 m to the uppermost samples (952.1 m). To assess the robustness and metric independence of this classification, an alternative *birese* subdivision strategy was tested using a comparison function based on Euclidean distances between centroids of standardised diversity indices. This alternative approach supported the original classification pattern (see supplementary materials in Rinkevičiūtė et al., 2025).

The Bayesian age–depth model constructed (Fig. 37 A) was used to estimate the durations of the Mulde/*lundgreni* stages (Fig. 37 B–E) and to calculate the Nyquist frequency (see supplementary material of Rinkevičiūtė et al., 2025). The estimated duration distributions for all stages of the Mulde/*lundgreni* event were positively skewed (Fig. 37 B, C). Median and 95% highest density interval (HDI) estimates were as follows: Collapse – 50 ka (11–171 ka), Maximal Stress – 120 ka (31–601 ka), Recovery – 80 ka (21–576 ka), and the entire event – 260 ka (100–1136 ka). The Nyquist frequency of the sampling resolution (median: 13 ka; 95% HDI: 2.5–74 ka) was adequate to resolve these temporal dynamics (see supplementary material of (Rinkevičiūtė et al., 2025) for a more detailed argumentation).

Ostracod assemblages assigned to different stages of the Mulde/*lundgreni* event exhibited distinct distributions in bootstrapped sample means of diversity indices and abundance (Fig. 38). Ostracod populations from the Maximal Stress stage were characterised by markedly low diversity and abundance. Assemblages from the Collapse and Recovery stages exhibited reduced total abundance, lower inverse Simpson index values, and higher evenness compared to populations in equilibrium state outside the Mulde/*lundgreni* event interval.

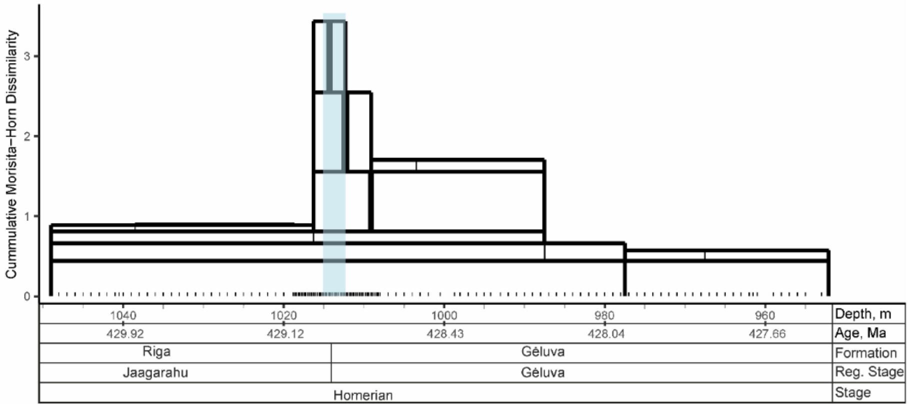


Figure 36. Hierarchical segmentation of ostracod assemblages from the Gėluva-118 core. Each rectangle represents a stratigraphic segment defined by shifts in assemblage composition. The base rectangle encompasses the full section, with higher rectangles indicating further subdivisions. Vertical lines mark the split points of lowest Morisita–Horn similarity within each segment; their width and the rectangle height both reflect the degree of compositional dissimilarity (1 – Morisita–Horn similarity). Taller and wider vertical lines indicate stronger contrasts. Cumulative dissimilarity values can be read on the vertical axis. Sampling positions are indicated by short ticks along the bottom. The light-blue zone marks the Maximal Stress stage. A ca. 80 cm offset between the Maximal Stress onset and the split of the tallest segment results from the requirement that segments include a minimum of 10 samples—an artefact that only affects narrow, sparsely sampled intervals and does not influence the broader delineation of the Mulde/*lundgreni* Event. Reproduced from Rinkevičiūtė et al. (2025), licensed under CC BY 4.0 (http://creativecommons.org/licenses/by/4.0/).

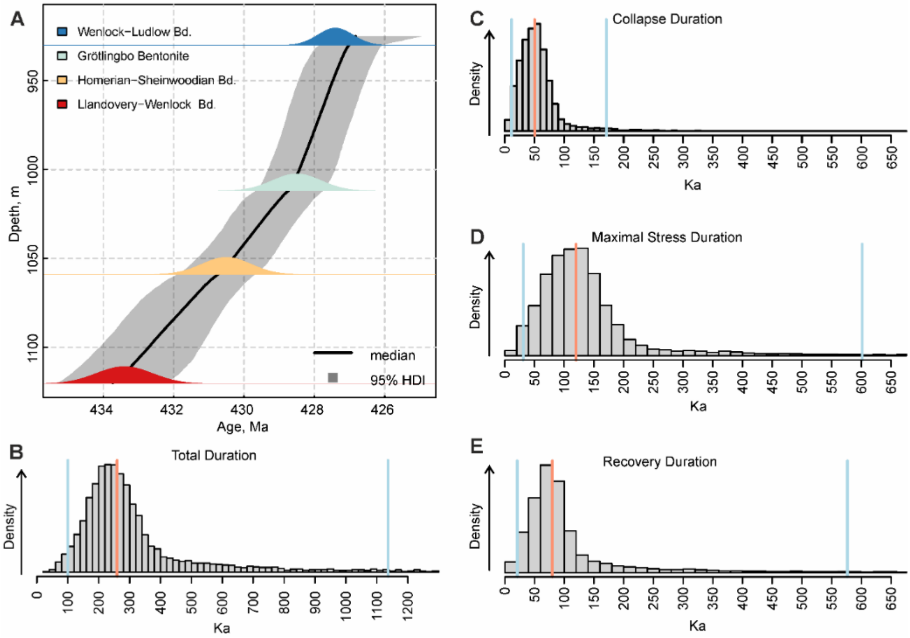


Figure 37. Bayesian age–depth model for the Gėluva-118 section (A), and estimated durations derived from it for (B) the entire Mulde/lundgreni event, and (C–E) its individual stages. The light-blue lines in panels B–E represent the 95% highest density interval (HDI), while the orange line indicates the median, i.e. the most probable duration. Reproduced from Rinkevičiūtė et al. (2025), licensed under CC BY 4.0 (http://creativecommons.org/licenses/by/4.0/).

Early Homerian assemblages from the Pre-Event interval (Old Equilibrium in Fig. 38) displayed lower inverse Simpson index values, slightly reduced total abundance, and lower evenness than those from the late Homerian (New Equilibrium in Fig. 38). A similar relationship was observed between ostracod populations of the Collapse and Recovery stages, respectively. The relationship between evenness and the inverse Simpson index varied between the two equilibrium states: Old Equilibrium assemblages exhibited greater variability in evenness, whereas New Equilibrium assemblages showed more variation in the inverse Simpson index (Fig. 38 A). Recovery assemblages were characterised by bi- or tri-modal distributions in diversity index densities. Due to limited sample size, such distributional features could not be robustly assessed for the Collapse stage.

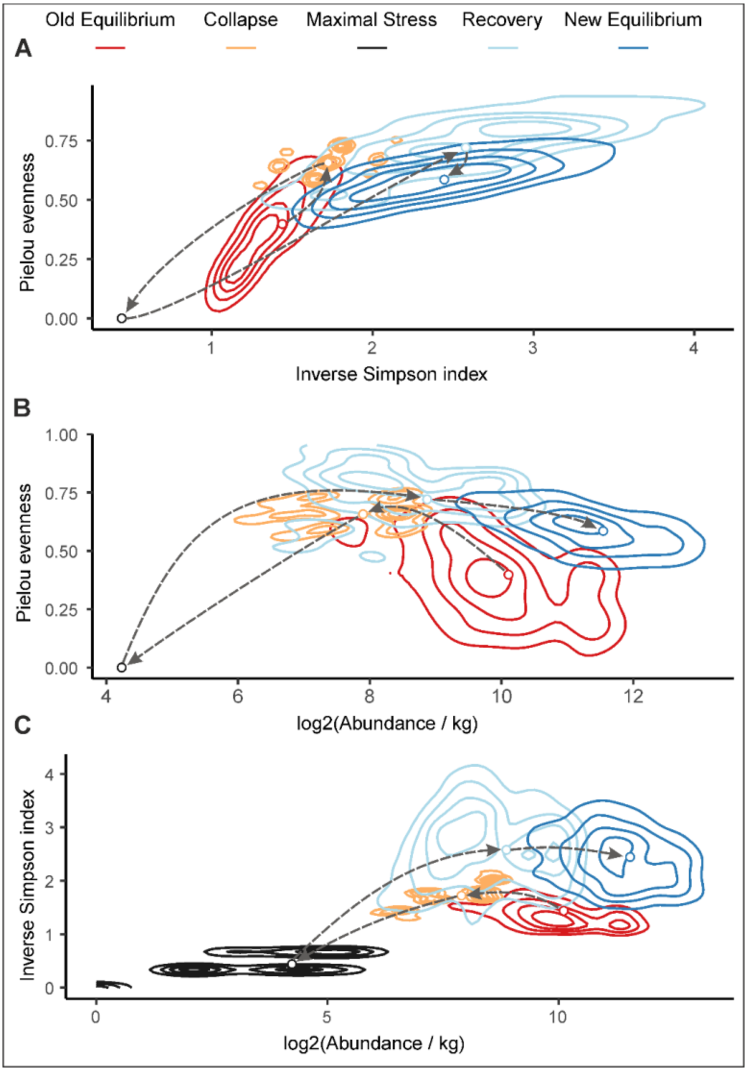


Figure 38. Contour plots showing bootstrapped sample means of diversity indices for ostracod populations at successive stages of the Mulde/*lundgreni* event. Points mark the centroids of the distributions, connected by arrows indicating chronological progression. Each stage is represented by four contour lines, dividing the range of empirical probability density distribution into five equal intervals. Reproduced from Rinkevičiūtė et al. (2025), licensed under CC BY 4.0 (http://creativecommons.org/licenses/by/4.0/).

Discussion

The Mulde/*lundgreni* event, initially characterised as a prolonged multi-phase extinction–recovery episode lasting ~1 Myr (Cramer et al., 2012), is now thought to have been much shorter. New data on graptolites, conodonts, and acritarchs suggest that extinction and recovery occurred nearly simultaneously (Radzevičius et al., 2016; Rinkevičiūtė et al., 2025; Venckutė-Aleksienė et al., 2016). Diversity loss in microphytoplankton was limited (Venckutė-Aleksienė et al., 2016), although a significant reduction in cyst size among dominant sphaeromorphs indicates decreased nutrient availability (A. Spiridonov et al., 2017), possibly linked to reduced ocean mixing (Rinkevičiūtė et al., 2025; Whittingham et al., 2022). Graptolite extinctions and subsequent radiations appear rapid and restricted to a narrow interval (Rinkevičiūtė et al., 2025; Whittingham et al., 2020).

Initial interpretations based on Gotland conodont data proposed a stepwise recovery of new taxa (Rinkevičiūtė et al., 2025). However, later studies in Baltica and Bohemia demonstrated that these species originated nearly simultaneously but spread asynchronously across regions, supporting a 'delay phase' turnover model (Radzevičius, Spiridonov, & Brazauskas, 2014; Radzevičius et al., 2016; Radzevičius, Spiridonov, Brazauskas, et al., 2014; Rinkevičiūtė et al., 2025; Slavík, 2014). This apparent stepwise origination reflects spatial heterogeneity and stratigraphic incompleteness rather than biological sequence. Recurrence-based analyses from Polish and Lithuanian sections further support rapid and severe turnover, marked by a sharp decline in conodont abundance and a shift towards simpler community dynamics (Jarochowska & Munnecke, 2016; Radzevičius et al., 2016; Radzevičius, Spiridonov, Brazauskas, et al., 2014; Rinkevičiūtė et al., 2025; Spiridonov, 2017). These patterns align well with coordinated stasis theory, which posits rapid macroevolutionary restructuring during brief global perturbations (Brett, 2012).

The present study, based on a high-resolution ostracod dataset, provided a detailed bed-by-bed characterisation of the Mulde/*lundgreni* biotic transition, capturing the decline, stress interval, and recovery phases. It confirmed the abrupt (Fig. 37) and severe (Fig. 38) nature of the Mulde/*lundgreni* event, demonstrating that benthic fauna—specifically ostracods—were dramatically affected. These new results are significant considering that research on the Mulde/*lundgreni* event has predominantly focused on pelagic taxa, with benthic groups remaining underrepresented (Calner et al., 2012; Rinkevičiūtė et al., 2025).

Previous studies report minimal changes in benthic clades during the Maximal Stress interval, potentially due to lower temporal resolution or the event's brevity (Jeppsson et al., 1995). Additionally, it has been suggested that observed patterns might reflect stratigraphic artefacts resulting from lateral facies shifts during major sea-level changes (Jarochowska & Munnecke, 2016; Rinkevičiūtė et al., 2025). However, ostracods—typically abundant in well-oxygenated shallow-water settings—showed sharp declines in abundance during the Maximal Stress interval, with some samples becoming entirely barren. Stratigraphically, this barren level aligns with the laminated, microfossil-poor Ančia Member in distal deep-water facies of the Baltic Basin (Radzevičius, Andrej, et al., 2014; Rinkevičiūtė et al., 2025), indicating widespread environmental stress, potentially linked to anoxia or toxicity across the water column.

Although no ostracod species were entirely extirpated at the section scale, the event caused pronounced shifts in their abundance and community structure. This reflects an ecosystem-level tipping point, followed by prolonged community stasis lasting up to approximately 260 kyr, mirroring patterns of short-term coordinated stasis (Brett, 2012; Rinkevičiūtė et al., 2025). A comparable synchronous turnover was observed in conodonts, though in an opposite direction—towards reduced abundance and diversity with increased evenness (Rinkevičiūtė et al., 2025; Spiridonov, 2017; A. Spiridonov et al., 2017). Changes in graptolite zooplankton, key agents in marine nutrient cycling, may have driven such broad ecological restructuring by influencing ecosystem dynamics across spatial and trophic scales.

The observed patterns in abundance and diversity indices indicate that the Maximal Stress stage represents a distinct interval of maximal ecological disruption (Fig. 38). Diversity dynamics across the other event stages appear to have been shaped primarily by two factors: ecological stress and the ‘pull of equilibrium’. Stress differentiates equilibrium from transitional communities, contributing to reduced abundance and increased evenness during both Collapse and Recovery stages. The ‘pull of equilibrium’ stabilises transitional communities, anchoring them to their preceding or succeeding equilibrium states and limiting compositional shifts—except during the Maximal Stress stage, where total collapse enables transition to a new equilibrium. Old Equilibrium communities displayed lower diversity and more variable evenness (Fig. 38 A), implying less stable dominance structures where small richness changes significantly affected evenness. Conversely, New Equilibrium communities exhibited higher richness and more stable dominance structures, with evenness less influenced by fluctuations in richness (Fig. 38 A). These patterns may reflect a post-event emergence of ecologically more mature, species-saturated ostracod communities. Furthermore, the bi- or tri-modal distributions observed in the Recovery stage suggest that returning to equilibrium may have involved multiple disturbance and stabilisation phases.

Fig. 36 can be interpreted as a temporal cross-section through a spatiotemporal Bretskyan-like hierarchy and its constituent entities (for a definition, see section *Defining Bretskyan Entities from Empirical Data: Key Observables, Spatial Properties, and Limitations*). The observed patterns in diversity metrics, as well as the distribution of partitions and their strength variations along the Gėluva-118 section, suggest that the Mulde/*lundgreni* Event Maximal Stress interval likely marks the boundary between two large-scale geobiomes, each comprising smaller-scale geobiomes. For example, the identified Old Equilibrium and Collapse Bretskyan-like entities are nested within a broader Old Equilibrium + Collapse Bretskyan-like entity. Given that this event is globally recognised, geobiomes at all scales likely underwent transformation during this interval. However, the temporal window covered in this study is relatively narrow and considerably less than the ~40 Ma threshold above which marine biota achieves global synchronisation, spatial genealogical mixing, and predominantly internally organised dynamics (Spiridonov & Lovejoy, 2022). Consequently, it is unlikely that this study captures a full cross-section through a global Bretskyan unit (Gaia). Instead, the identified Bretskyan-like entities most likely represent regional to local-scale geobiomes nested within the larger Silurian Baltic Basin marine geobiome.

Assuming a positive relationship between geobiome duration and size (Spiridonov & Eldredge, 2024), the brevity of the Collapse and Recovery phases, in contrast to the more extended durations of the Old and New Equilibrium intervals, suggests that during biotic perturbations—such as the Mulde/*lundgreni* events—spatially extensive, long-lived, and relatively stable geobiomes disintegrate and fragment into multiple, smaller, short-lived, and less stable geobiomes, as exemplified by the Collapse and Recovery Bretskyan-like entities. The possibility and nature of such geobiome dynamics were discussed in *Barrier Dynamics Over Time and Mass Extinctions* section. Accordingly, this study offers empirical support for a notable spatiotemporal pattern anticipated within the evolutionary framework of the anastomosing Bretskyan hierarchy, suggesting that further research is warranted.

As this study focuses on a single taxonomic group and core section, the findings should be regarded as provisional and would benefit from further comparative analyses across additional sites within the Silurian Baltic Basin and beyond. The reliability of the Mulde/*lundgreni* event reconstruction in this study also depends on the stratigraphic completeness of the Gėluva-118 core. However, the presence of a characteristic two-peaked positive $\delta^{13}C$ anomaly in the Gėluva-118 core suggests a relatively complete record of the event. A stratigraphic gap would likely obscure or truncate this signal (Radzevičius et al., 2017; Rinkevičiūtė et al., 2025; Rinkevičiūtė et al., 2022). Additional support for completeness and reliability includes the presence of graptolite index species in expected intervals relative to the isotope curve (Radzevičius, Spiridonov, & Brazauskas, 2014; Rinkevičiūtė et al., 2025; Rinkevičiūtė et al., 2022), the gradual variation of clay content in generally unchanging lithology, the continuity and clarity of the observed transitions between event stages (Fig. 38), and the distinct taxonomic composition of ostracod assemblages sampled at 0.2 m resolution—suggesting minimal time-averaging and good preservation of original community structure.

Conclusion

The mid-Homerian extinction and biotic turnover, though historically recognised primarily from pelagic indicator groups such as graptolites and conodonts, was also clearly expressed in shallow shelf benthic communities. Using a high-resolution ostracod dataset and Bayesian age–depth modelling, the total duration of the Mulde/*lundgreni* event was estimated at approximately 260 ka. This duration coincides with the regressive phase of a 4th-order sea-level cycle (Radzevičius et al., 2017), aligning closely with half of the 405 ka long eccentricity cycle. In contrast to earlier estimates suggesting a ~1 Myr duration for the full extinction-to-recovery interval (Cramer et al., 2012), the Gėluva-118 record indicates a significantly shorter event, including both collapse and recovery phases.

The collapse and subsequent reorganisation of ostracod assemblages occurred over timescales similar to those of major Quaternary glaciations. The ensuing stabilisation phase supports the applicability of the coordinated stasis model (Brett, 2012) to mid-Palaeozoic marine benthos. These findings confirm that the Mulde/*lundgreni* event was both rapid and widespread, with comparably paced turnover dynamics in both benthic and pelagic marine realms. The findings also suggest that such abrupt biotic perturbations are likely to fragment large-scale, durable, long-lasting geobiomes into smaller-scale, less stable and transient geobiomes.

In light of these findings, the HespDiv method *birese* emerges as a useful and powerful tool for identifying and characterising critical transitions in community dynamics, providing a temporal cross-section through Bretskyan-like entities. Moreover, the methodology demonstrated in this case study can be effectively applied to palaeontological datasets from other sections, including areas beyond the Silurian Baltic Basin, to investigate the synchronicity of the Mulde/*lundgreni* event extinction and subsequent recovery. Research into other biotic events could similarly benefit from the quantitative approaches employed here.

3.4. Evaluating HespDiv Methods

In the second chapter of this thesis, Bretskyan hierarchy theory was identified as a conceptual framework with significant, yet largely untapped, potential for explicating the spatial and temporal organisation of geobiological systems. The concept of patch-based, nested, dynamic hierarchies pervasive across all kinds of natural systems was also introduced. In light of the theoretical importance of Bretskyan hierarchy, the effectiveness of HespDiv methods may be gauged by their capacity to investigate and reveal the structure of Bretskyan systems—with added value if they are also applicable to these similarly structured, patch-based systems. This section will address that issue.

In the third chapter of the thesis, a range of traditional methods for analysing the spatiotemporal organisation of biota was reviewed. Therefore, if the HespDiv methods are to be considered successful, they should not only be suitable for studying Bretskyan systems but should also surpass commonly used alternatives in their ability to do so. A comparison with these alternatives will thus be provided.

Finally, in the third chapter of the thesis, the HespDiv method family was introduced, along with the two newly developed HespDiv methods and their respective case studies. These case studies have already demonstrated the methods' utility. Accordingly, this section will now evaluate the usefulness of their defining characteristics.

3.4.1. Alignment with Bretskyan Principles

To begin, it is useful to recall how Bretskyan hierarchy units are defined. These units are characterised by several essential features: they are spatially and temporally distinct; hierarchically nested, with smaller units forming strict subsets of larger ones; and differentiated by both ecological and genealogical criteria. Genealogy, in particular, necessitates spatial contiguity, as genetically distinct communities may arise even under similar ecological conditions if separated by distance and shaped by different local histories. As such, Bretskyan units are explicitly bounded geographically by dispersal barriers. The design of the *hespdiv* algorithm inherently produces subdivisions that align with these defining characteristics, making it particularly suitable for studying Bretskyan hierarchical structures.

In terms of methodological properties, both *hespdiv* and *birese* satisfy most of the essential criteria for identifying Bretskyan entities—criteria that are often only partially met or entirely lacking in traditional approaches.

Specifically, both methods (1) produce hierarchically organised bioregions or temporal intervals; (2) generate subdivisions that are spatially or temporally contiguous; (3) define boundaries explicitly in spatial or temporal domains; (4) integrate effectively with ecological metrics and community similarity functions, preserving their raw outputs to enhance interpretability; and (5) demonstrate high flexibility, accommodating diverse data types and subdivision criteria, including user-defined comparison functions.

3.4.2 Comparison with Traditional Bioregionalisation Methods

The advantages listed above are summarised in a broader methodological comparison (Table 2), which contrasts *hespdiv* and *birese* with five commonly used approaches: hierarchical cluster analysis, ordination methods, network analysis, wombling, and split moving-window techniques. While some of these methods align partially with Bretskyan principles—such as producing hierarchical structures or incorporating spatial and temporal information—none satisfy all defining criteria simultaneously. Most of them lack integrated support for raw fossil occurrence data or the ability to delineate spatially contiguous bioregions. HespDiv methods compare pooled bioregion or temporal interval samples using a selected comparison function (e.g. some well-established ecological similarity metric like Jaccard or Morisita-Horn). This overcomes the issue of reliance on sample-to-sample distance matrix entries, that are often biased by small and unequal sample sizes. Furthermore, unlike HespDiv methods, traditional approaches often do not generate explicit spatial or temporal boundaries, nor do they reflect the hierarchical relationships among the resulting units.

Interpretability and Integration with Ecological Metrics

In terms of interpretability, HespDiv methods also stand out as among the most transparent. For instance, traditional approaches such as cluster analysis, network analysis, or ordination techniques allow bioregionalisation based on ecological similarity metrics like Morisita-Horn, Jaccard, or Sørensen. However, these metrics are typically applied during pre-processing, by computing a (dis)similarity matrix in advance of the main analysis. Consequently, while the final output may reflect how (dis)similar bioregions are, it does so in relative terms, without reporting absolute (dis)similarity values between bioregions in the results. By contrast, HespDiv methods integrate similarity metrics directly into the subdivision process, preserving the raw similarity values between bioregions. This results in clearer, more interpretable outputs, directly tied to widely recognised ecological metrics.

Table. 2. Comparison of HespDiv methods with other approaches.

	hespdiv	***birese***	**Hierarchical Cluster Analysis**	**Ordination Methods**	**Network analysis**	**Wombling**	**Split Moving Window**
Hierarchical?	Yes	Yes	Yes	No	Yes[1]	No	Yes[2]
Output boundaries?	Yes	Yes	Yes[3]	No	No	Yes	Yes
Produce contiguous clusters?	Yes	Yes	Yes[4]	No	No	No	Yes[5]
Support raw fossil occurrence or abundance data as input?	Yes	Yes	No	No	No	Yes[6]	Yes
Incorporates temporal or geographical information?	Yes	Yes	Yes[7]	No	No	Yes	Yes
Cluster separation is reflected by:	Values of a comparison function and structure of a spatial dendrogram	Values of a comparison function and structure of stacked rectangles representing section segments	Values of a linkage function and structure of a dendrogram	Proximity of points in ordination space	Proximity of clusters; number and density of edges between and inside clusters	Clusters are not identified	Values of a distance function

[1] *Some network-based methods incorporate hierarchical elements(e.g. Newman, 2012).*

While some approaches are capable of producing hierarchical outputs (e.g. Cornelius & Reynolds, 1991), the computations involved are not inherently hierarchical and do not dynamically adjust their scale in the way that HespDiv methods do (see section on Characteristics of HespDiv Family Methods)

[3] *Methods that use predefined geographic units such as grid cells or continental boundaries can delineate spatial regions, but the shapes and sizes of these units are determined a priori (e.g. Kreft & Jetz, 2010).*

[4] *Certain hierarchical clustering techniques (e.g. Duque et al., 2007; Legendre & Legendre, 2012b) generate, or have the capacity to generate, clusters that are spatially contiguous (see also Gibert et al., 2022).*

[5] *In the case of split mowing window approaches, spatial clusters would only be formed along the predefined transect being analysed.*

[6] *Categorical wombling (e.g.Oden et al., 1993) may be applied to raw fossil data when each spatial unit contains a single taxonomic occurrence. However, the large number of taxa and their uneven distribution can hinder performance. Binary wombling could instead be carried out for each species' presence/absence data, followed by boundary analysis (e.g. Davis & Gagné, 2018; Fortin, 1994), but such approaches are limited by the nature of absences in fossil records.*

[7] Some hierarchical clustering methods incorporate geographic information directly (e.g. *Duque et al., 2007; Gibert et al., 2022; Legendre & Legendre, 2012b*).

The strength of this integration becomes particularly apparent in datasets with a high prevalence of singletons (i.e. localities containing only a single fossil occurrence), which are common in terrestrial macrofaunal records. When datasets consist exclusively of singletons, precomputed (dis)similarity matrices will yield identical values for a wide range of ecological metrics (see Table 1 in the Cluster-Based Methods section). This redundancy effectively nullifies the distinct theoretical perspectives offered by different ecological metrics, as results across different traditional methods will converge. In contrast, HespDiv methods apply these metrics dynamically during the subdivision process, preserving their mathematical and conceptual distinctions. This enables more meaningful comparisons and interpretations, even in datasets dominated by singleton localities.

Flexibility

High methodological flexibility—stemming from the ability to employ custom-defined comparison functions and accommodate various data types and structures—represents a major advancement over traditional approaches. The manual definition of comparison functions enables users to implement alternative subdivision strategies beyond those pre-set in the "hespdiv" package (e.g. those based on reductions in Sørensen similarity, Jaccard similarity, Morisita-Horn similarity, Morisita similarity, or Pielou entropy). This customisability allows comparison functions to be tailored to the expected structure and type of input data, offering several key advantages.

First, it facilitates the testing of result robustness under different subdivision strategies and data perspectives. Such an application was demonstrated in the *birese* case study: initially, the Gėluva-118 section was subdivided using ostracod abundance data and a comparison function based on Morisita-Horn similarity. Subsequently, an alternative subdivision was attempted using a dataset of ostracod diversity indices and a custom-made comparison function that computed Euclidean distances between the centroids of those indices (see supplementary material of Rinkevičiūtė et al., 2025). Despite the differing subdivision approaches—one based on community composition, the other on diversity metrics—the segmentation results were nearly identical, suggesting robustness.

Secondly, custom-made comparison functions enable the exploration of aspects of spatial and temporal biotic organisation that go beyond those addressed by Bretskyan hierarchy theory, which primarily emphasises spatially and temporally stable intertaxic associations. A complementary perspective focuses on the stability of associations between taxonomic occurrences and environmental variables—that is, the delineation of regions where such associations remain consistent. Investigating taxon–environment relationships is the central objective of species distribution modelling and ecological niche modelling (Daumantas, 2022). Empirical evidence from these fields indicates that species–environment relationships can vary geographically (Fitzpatrick et al., 2007). Neglecting this spatial variation in modelling studies can lead to misleading conclusions, whereby relationships identified at a global scale are reversed or obscured at local or regional levels. This issue represents a spatial instance of Simpson's paradox, wherein relationships observed within subsets of data are contradicted or masked when the data are aggregated (Simpson, 1951). In a spatial Simpson's paradox, a particular statistical relationship observed in data depends on location, as well as spatial scope and scale (e.g. local, regional, global).

Simpson's paradox was encountered in a previous study investigating the evolution of prehistoric human settlement patterns in Lithuania. It was recognised that the influence of local environmental factors on settlement distribution varied spatially and was contingent upon broader environmental and techno-socio-economic-cultural contexts (Daumantas et al., 2020). To circumvent this problem, regional-scale variables were employed. However, the *hespdiv* method, through its support for user-defined comparison functions, provides the capacity to delineate areas within which the associations between settlements and local environmental conditions are statistically uniform and different from those in other areas. A comparison function for such a study could, for example, construct predictive models of settlement distribution for each region being compared and assess either the similarity of model structures or the magnitude of extrapolation errors. Boundaries separating areas with markedly different model structures or large extrapolation errors would indicate spatial transitions in human–environment associations—that is, regions where settlement distribution rules shift. Comparable applications could be envisioned for palaeontological, ecological datasets. Moreover, such applications would also be profitable in geosciences, as geoscientific datasets are no more free Simpson's paradox than presented biotic cases. For example, the paradox is very apparent in the relationship between magnetic susceptibility of soils and rainfall amounts as the relationship in global data is weak and complicated, while at the same time in some regions it can become very deterministic, turning magnetic susceptibility into a reasonable rainfall proxy (Balsam et al., 2011). Thus, delineations such of regions of uniform, deterministic relationship would be a necessary prerequisite to practically use take advantage of such new proxies. Even the macroevolutionary dynamics exhibit the changing functional relations as a function of scale: for example diversity-climate relations are time scale-dependent (Spiridonov & Lovejoy, 2022).

At present, there are no established methods designed to explicitly detect spatial variation in species distribution or ecological niche models. Similarly, *birese* could be applied to temporal datasets to identify intervals characterised by uniform statistical relationships between biotic and abiotic factors. Consequently, *hespdiv* and *birese* may serve as novel tools for exploring the organisation of spatial and temporal biotic systems and for addressing manifestations of Simpson's paradox in both spatial and temporal contexts.

Thirdly, independence from specific data types and structures greatly enhances the utility and application scope of these methods. For example, the pre-set *hespdiv* methods are designed to work with fossil occurrence data formatted as R vectors of taxonomic names or identifiers. However, *hespdiv* supports not only vectors but also data frames, matrices, lists, time series, and other data structures that can be subset using the indexing operators [ ], [[ ]], or [,]. With minor adjustments, a pre-set comparison function can thus be modified to support other common palaeontological data types, such as abundance data or collection-based formats.

This versatility, combined with the ability to define custom comparison functions, is especially valuable for the study of other natural patch-based hierarchical systems topologically akin to Bretskyan hierarchy (see *The Apparent Order of Patches and Smoothness, and Entities as Patches* section). It enables analysis of non-biological datasets—e.g. geochemical, sedimentological, or other geological data—thereby revealing regions where abiotic systems exhibit coherent evolutionary trajectories. Although the study of abiotic data falls outside the scope of this thesis, the ability to analyse similar patch-based, dynamic, nested hierarchical systems is important for encouraging broader adoption of the HespDiv framework, which could in turn accelerate methodological development—an outcome beneficial to this thesis and to the field more generally. Moreover, such studies may deepen our general understanding of patch-based, nested, dynamic hierarchies, of which the Bretskyan hierarchy represents a particular instance.

In summary, input data flexibility is fundamental for the application of HespDiv methods to diverse palaeontological datasets, for the continued development and adoption of the methodology, and for advancing theoretical insights into Bretskyan hierarchy and topologically related patch-based, nested, dynamic hierarchies.

3.4.3. Post-Processing Options and Integration with Downstream Analyses

The “hespdiv” package infrastructure further enhances interpretability and analytical rigour by including tools to assess the statistical significance of split-lines, evaluate the sensitivity of resulting polygons and clusters to input variation, and support other diverse visualisation and post-processing options (see *hespdiv* section). This is particularly valuable when analysing intracontinental-scale Bretskyan entities, which may display fuzzy or probabilistically defined boundaries (Spiridonov & Eldredge, 2024). Such sensitivity analysis also counteracts the more general limitation of compositional hierarchies stemming from the strict part-whole relationship requirement (See Limitations of Bretskyan Hierarchy Theory section). Thus, the capacity to distinguish between well-defined and diffuse geobiomes marks a significant methodological advantage. In contrast, traditional bioregionalisation methods generally lack such integrated diagnostics; significance is typically assessed via external procedures, such as ANOSIM or SIMPER (see Bioregion Analysis Methods section).

The HespDiv polygons obtained can serve as territorial sampling units in subsequent studies. For instance, historical biogeography methods such as DEC or DIVA (see Historical Biogeography Methods section) require predefined areal units as input. In continental settings, defining such units a *priori* can be challenging and subjective without specialised tools. The *hespdiv* method provides precisely such a tool, offering objective definitions of areal units. Using the diagnostic features available in the “hespdiv” package, it is possible to distinguish between insignificant, weak, and spatially unstable boundaries and those that are statistically robust and reliable. Applying *hespdiv* analysis to consecutive time intervals could reveal temporal shifts in spatial biotic structuring, while applying historical biogeography methods to the resulting HespDiv polygons—using the same occurrence dataset—could help identify the biogeographical processes and taxa responsible for the observed changes. Such integrative studies represent a promising avenue for advancing our understanding of spatiotemporal biotic organisation.

3.4.4. Conclusion

Although both case studies demonstrated that HespDiv methods yield meaningful and valuable results, a systematic comparison with traditional approaches—within a controlled comparative study design—has not yet been conducted. Nevertheless, their methodological alignment with Bretskyan principles, along with the tangible advantages offered by their additional features, already provides a strong rationale for their application in studies of hierarchical biogeographical organisation and related fields.

3.5. Future Prospects and Developments

Although the previous evaluation of HespDiv methods suggests that they are valuable and have potential for wide application beyond studies of systems organised according to the Bretskyan hierarchy, these methods still offer substantial room for improvement. The current state of development should be viewed primarily as foundational, providing opportunities for future expansion and refinement.

Several key directions have been identified for future enhancement of HespDiv family methods, including efficiency, robustness, performance (and consequently broader applicability), and output post-processing capabilities that enhance result interpretability. Additionally, more case studies are essential to fully understand potential limitations and strengths.

3.5.1. Parallel Processing and Algorithmic Structure

Parallel computation can significantly reduce processing times for large or complex computational tasks by distributing workloads across multiple CPU cores (or GPUs in specific scenarios). As multi-core computers become increasingly affordable and widespread, these time reductions can become substantial. R offers several powerful packages for parallel computing, such as “parallel” (Team, 2019) or “future” (Bengtsson, 2021; Bengtsson, 2025). The “future” package has already been used successfully in the development of a new sensitivity analysis function for *hespdiv*, which tests sensitivity to data without recursion. Specifically, rather than identifying an entirely new hierarchical subdivision structure, the function identifies new optimal split-lines within each polygon based on different sample subsets. The application of parallel processing in this function has resulted in approximately a 10-fold reduction in computation times on a machine equipped with 48 cores (currently, this new function is only available in the newfeatures branch of the Liudas-Dau/hespdiv GitHub repository).

However, the current implementation of the *hespdiv* method in R is recursive, whereas parallelisation in R is mostly feasible for iterative or independent tasks. Additionally, the recursive nature of the algorithm complicates and hinders its development, debugging and maintenance, as well as adds to the waste of computation resources. This is primarily due to stack overflow errors triggered by excessive recursion depths, which are challenging to debug. These errors are not catchable using standard functions like tryCatch() and when they occur, they can cause R session crashes and data loss; moreover, their traceback messages are typically truncated, making it difficult to pinpoint the exact lines of code responsible.

Therefore, translating the *hespdiv* algorithm into an iterative structure could greatly enhance its efficiency and robustness. This iterative approach was successfully applied during the development of the *birese* algorithm: rather than making recursive segment-subdivision calls, it uses a while loop with a dynamically expanding and contracting queue of inputs for segment subdivision (see the supplementary material in Rinkevičiūtė et al., 2025). This iterative algorithm also lends itself to further optimisation through parallel processing, enabling the expanding queue of subdivision inputs to be handled significantly faster. In such designs, enhanced by parallelisation, each pair of segments or polygons resulting from an established partition would be subdivided concurrently rather than sequentially. Additionally, parallel processing could further reduce computation time if applied within recursion or iteration loops themselves, accelerating tasks such as boundary generation and testing.

3.5.2. Boundary Generation Challenges and Alternatives

Beyond parallel computing and restructuring the algorithm into an iterative design with dynamically expanding inputs, further increases in computational efficiency, performance and breadth of applicability could be achieved by altering the approach to boundary generation and subsequent data filtering. In this regard, the subsequently developed *birese* algorithm already demonstrates superiority compared to *hespdiv*, since it places split-points at the midpoints between consecutive observations along the transect. This strategy results in a minimal set of informative split-points, each of which contributes to a unique subdivision, exhausting all their possibilities.

Inefficiencies of Current Split-Line Generation

In contrast, the current *hespdiv* algorithm may generate and test redundant split-lines—lines that differ spatially yet yield identical data partitions—thus wasting computational resources and increasing runtime unnecessarily. Moreover, although not directly related to computational efficiency but rather to the performance and the breadth of applicability, the current method of generating split-lines explores only a subset of all potential unique data partitions. Consequently, certain spatial hierarchies remain irrecoverable because the present implementation cannot distinguish some boundaries. For instance, it cannot directly identify isolated ("island") clusters that reside fully within another cluster without intersecting its boundaries. Additionally, the current *hespdiv* approach is not ideally suited for global datasets, since opposite edges in two-dimensional global data projections represent adjacent areas that would be artificially separated before analysis begins under the current *hespdiv* algorithm.

Furthermore, generating both linear and nonlinear split-lines and using them for polygon partitioning and spatial data filtering involves complex spatial operations, including numerous split-line geometry validations and polygon geometry standardisations. These operations considerably extend computation times. The number, shape, and placement of split-lines produced by the current algorithm also depend heavily on the shape of the input polygon. Consequently, areas with complex configurations—such as the Mediterranean Sea with its numerous peninsulas and islands—pose particular challenges to *hespdiv* implementations.

Advantages of Thiessen Polygon-Based Approaches

Considering the limitations of current split-sine generation algorithm, significant benefits could be realised by developing a spatial HespDiv method that creates boundaries analogous to those produced by the *birese* approach.

The two-dimensional analogue to midpoints between consecutive observations along a transect would be lines drawn through spatial midpoints between pairs of nearest-neighbour observation points. Such lines constitute the vertices of Thiessen polygons. Joining these lines into closed loops would yield boundaries that define spatially contiguous sets of observations. The complete set of loops formed from all unique combinations of these adjacent lines would represent every possible way to subdivide the dataset into spatially contiguous clusters. This approach would enable the detection of "island" clusters and would overcome performance issues related to complex study area shapes; in fact, complex area polygons would reduce the total number of contiguous clusters, thus decreasing computation time. Consequently, such a modification to the algorithm would render it significantly more efficient (eliminating redundant partitions), comprehensive (exploring all unique partitions), and robust across a broader range of scenarios, including intricate study area configurations and isolated ("island") clusters. However, certain optimisation techniques would be essential, as exhaustive testing of all possible partitions would not be feasible in most practical cases.

Moreover, an additional promising aspect is that observations sharing a Thiessen polygon boundary could be considered spatially adjacent. This adjacency information could be obtained through Delaunay triangulation and subsequently encoded into a spatial adjacency matrix, similar to methods employed in spatially constrained hierarchical clustering analyses (Legendre & Legendre, 2012b). Valid, spatially contiguous clusters could then be derived by processing this adjacency matrix, directly sampling adjacent observations to form contiguous groups. Sampling based on these adjacency relationships—rather than explicit construction and use of Thiessen polygons—would be functionally equivalent to the current approach of generating boundaries and filtering spatial data with them. As such, this would bypass the computationally intensive spatial geometry operations currently involved in *hespdiv* boundary generation, thereby significantly reducing computation times.

The construction of the adjacency matrix, based on Delaunay triangulation, would only need to be performed once, prior to initiating the recursive or iterative subdivision process. Similarly, the construction of boundaries defining HespDiv polygons would also be carried out just once, after the subdivision pattern has been established and encapsulated within the identified HespDiv clusters. HespDiv polygons could be generated by constructing Thiessen polygons from the occurrence locations and then merging the polygons of occurrences assigned to the same HespDiv cluster, retaining only the outer vertices to form boundary lines. Therefore, these algorithmic modifications would be highly efficient, as these computationally intensive steps would be executed only once, rather than being repeated at each subdivision.

Additionally, global-scale applications would benefit greatly from this methodological change, as the adjacency matrix or its construction could easily be adjusted to account for adjacency between observations situated on opposite edges of a two-dimensional global map projection.

Qualitatively different subdivisions, more closely aligned with Bretskyan hierarchy theory, could be obtained by partitioning spatiotemporal volumes rather than geographical spaces or temporal transects alone. The Thiessen polygon-based approach could readily be extended into the spatiotemporal domain by constructing Voronoi cells, the three-dimensional equivalent of two-dimensional Thiessen polygons, for which efficient algorithms already exist (Yan et al., 2010). Such cells are generated by placing planes at midpoints between closest points within a spatiotemporal volume. A notable advantage of this approach is that Voronoi cell construction would need to be performed only once, after which an analogous pairwise adjacency matrix could be derived. Subsequently, calculations would remain identical regardless of dimensionality, thereby avoiding additional complexity when transitioning from spatial or temporal analyses to spatiotemporal analyses. Currently, no bioregionalisation methods operate directly within both spatial and temporal domains simultaneously. Only wombling has been adapted to incorporate this capability (Halder et al., 2024); however, as a boundary detection method, it is unsuitable for addressing many bioregionalisation problems.

Limitations of Thiessen Polygon-Based Approaches

Although approaches based on Thiessen polygons appear very attractive, they would be inferior in some respects to the current implementation of the *hespdiv* algorithm. One significant limitation concerns how area size criteria, controlled by the arguments S.crit and S.crit.rel, would be affected. When subdivisions are forced to pass through midpoints between observations, each unique contiguous cluster can be distinguished by only a single boundary, resulting in a polygon with a single possible area size. If this area is smaller than required by the area size criteria, the subdivision would be disqualified without further consideration. However, in some instances, a slight shift of the boundary towards one of the observations could yield polygon areas satisfying the criteria. Given that the true ecological boundary location is unknown—although the most parsimonious assumption would place it midway between points with distinct taxonomic compositions—such minor shifts should be permissible. Allowing these adjustments, as *hespdiv* does, could enable polygons to meet area criteria and achieve more meaningful data partitions.

Another related limitation arises from sensitivity analyses. If sensitivity analyses indicate stable clusters and unchanging boundaries, it might create the false impression that boundary locations are confidently established. This could happen because, when boundary positions are constrained to a fixed set of paths, boundaries will not vary as long as identified clusters remain stable. In contrast, the current implementation of the "hespdiv" package permits separate sensitivity analyses of HespDiv clusters and polygons. Polygon (and consequently boundary) stability is typically much lower than cluster stability (compare Figs. 30 and 31), because spatially distinct boundaries may distinguish identical sets of observations. For example, if a boundary traversed a sparsely sampled region, such as the northwestern United States in the Miocene mammal bioregionalisation study (Fig. 30 C), *hespdiv* polygon sensitivity analysis would explicitly indicate uncertainty regarding the precise boundary location. A statistical significance of the boundary and associated stability of resulting clusters would therefore imply only that the boundary lies somewhere within that region. Conducting a similar sensitivity analysis using a Thiessen polygon-based algorithm would consistently produce boundaries passing through exactly the same locations, even in these uncertain scenarios. As a consequence, polygon and cluster sensitivity analyses would converge, resulting in the loss of information.

Furthermore, in some studies, the bioregion size distribution might be of particular interest. Using the current *hespdiv* algorithm, the distribution of polygon areas for stable clusters can be derived from cluster sensitivity analyses and the identification of analogous clusters (clusters sharing occurrences beyond a specified threshold). Conversely, employing a Thiessen polygon-based algorithm following a similar procedure would yield only a narrow set of point estimates for polygon sizes.

Finally, despite the current *hespdiv* boundary generation approach being computationally inefficient—generating redundant boundaries and not exploring all possible partitions—it still constitutes a practical heuristic. The current approach produces a sufficient number of boundaries to reliably identify optimal partitions (a conclusion drawn from observing that split-line performance is highly spatially autocorrelated and changes gradually across space), but not so many that more advanced heuristics in boundary exploration and optimisation would become necessary. A Thiessen polygon-based approach, in contrast, would consider all possible partitions, leading to a combinatorial explosion that is practically infeasible to fully explore. Thus, additional pruning and optimisation strategies would be required to make such an approach tractable.

In summary, while adopting a Thiessen polygon-based approach could offer substantial improvements for the *hespdiv* algorithm in many respects, certain advantages remain for retaining and using the current *hespdiv* algorithm as it is presently implemented.

3.5.3. Result Post-Processing Options

The effectiveness of HespDiv methods could be further improved by extending the existing infrastructure of the “hespdiv” package and enhancing its options for results post-processing. Such development is currently ongoing, with updates being continually added to the package even during the writing of this thesis. The package’s GitHub repository (Liudas-Dau/hespdiv) presently includes a dedicated branch named "newfeatures," where these additional capabilities are implemented. The newly developed functionalities are outlined within the subsection "Output and its Analysis: hespdiv package infrastructure" of the "hespdiv" section of this thesis.

Group Effects on Subdivision Patterns

Among these new features, the most promising is the ability to investigate how specific groups within the dataset influence the performance of individual split-lines and the overall subdivision pattern. Data groups can support particular split-lines or the subdivision scheme as a whole, oppose them, or remain neutral. Neutral or opposing groups might indicate either an absence of spatial structure, a weaker spatial structuring compared to other groups, or a spatial structure fundamentally different from the groups driving the primary subdivision pattern. The group labels required for this new analytical extension can be defined based on any meaningful classification system—such as taxonomy, habitat type, lifestyle, diet, mobility, body size, or trophic position. Several metrics have already been developed for conducting this kind of analysis, each providing distinct and complementary insights. However, the complete interpretation of their value will only be possible after further methodological development and the accompanying publications of dedicated studies.

Split-line performance variability

A further result post-processing option planned for future implementation is the analysis of local split-line strength. Currently, it is unclear how the performance of a split-line varies spatially—both along and across its length. As discussed in the section on Boundary Methods, open boundaries occur far more frequently in nature than closed boundaries. Moreover, the Miocene mammal bioregionalisation study in the USA demonstrated that the locations of split-lines are not self-explanatory. For instance, the second-rank split-line (number 4) was highly statistically significant (Fig. 28), exhibited a low Morisita–Horn similarity value (0.27; Fig. 27), identified two stable HespDiv clusters (numbers 8 and 21; Fig. 31), and itself proved stable (with clearly identifiable alternative boundaries dividing occurrences similarly; Fig. 30 C). Yet, it passed through a dense spatial cluster of occurrences in the central United States, dividing it into two parts (spatial cluster is visible in Fig. 27). Sensitivity analysis indicated robust support for this split-line trajectory, as seen from boundary convergence in the area of the occurrence cluster (Fig. 30 C).

However, there are no obvious dispersal barriers in this region—on the contrary, it comprises the Central Plains, where mammalian faunas might be expected to be homogeneous due to unrestricted dispersal and mixing radiating outward in all directions from the centre. This situation, along with other similar cases, highlights the importance of investigating local split-line strength and understanding exactly which occurrences contribute to its placement, trajectory, and shape.

Among several plausible explanations, split-line number 4 consistently crossed the central USA occurrence cluster because: (1) there was indeed a sharp, local taxonomic discontinuity within that cluster driven by unknown ecological or environmental factors; (2) a pronounced taxonomic discontinuity existed at a broader scale (Southeast vs Central Plains), reinforced by a moderate or low discontinuity at the local level within the occurrence cluster; or (3) there was a strong taxonomic discontinuity at the broad scale (Southeast vs Central Plains) unsupported locally by the central occurrence cluster, and the split-line passed through the cluster solely due to biases or artefacts of the algorithm such as constraints imposed by subdivision criteria (e.g., the required minimum 1:4 ratio of occurrences between resulting HespDiv clusters as defined by the default N.rel.crit criterion in this study). Under this scenario, excluding the central occurrences from the Southeast cluster could have reduced its number below this ratio threshold, making an ideal partition impossible.

Thus, understanding split-line performance spatial variability is crucial, as it allows differentiation between sharp, ecotone-like taxonomic discontinuities and gradual or stepwise large-scale transitions. Furthermore, this analysis could reveal split-lines whose placement or shape has been negatively influenced by subdivision criteria or other algorithm artefacts and biases rather than genuine biotic discontinuities.

Various additional functions could be developed within the "hespdiv" package to investigate the local strength of a split-line and to identify the occurrences contributing to its observed placement, location, and shape. The most flexible and straightforward approach to exploring these questions would involve a function that enables the interactive drawing of two polygons on a map, bounding the occurrences of interest. These polygons would then be used to filter occurrences and compare them using a specified comparison function. For example, using this approach one could delineate parts of a spatial cluster of occurrences that are oddly divided by the split-line, and the resulting comparison values could then be contrasted with those of the split-line itself.

Additionally, all occurrences on either side of the split-line, except those belonging to the spatial cluster, could be selected to assess whether large-scale differences alone drive the split-line's placement. This approach could also be extended to examine the effects of particular occurrence groups as defined in previous subsection.

Alternatively, a method based on the split moving-window technique could be implemented to provide automated solutions to similar questions.

Transects, positioned perpendicularly to the split-line at regular intervals of a specified length, could be placed. These transects would be split into two parts by the split-line, and the nearest occurrences on either side of the line could be assigned to the split transects. Comparison functions could then be applied to these data subsets, yielding local (dis)similarity values and revealing how the strength of the split-line varies along its length.

Techniques such as these could substantially enhance our understanding of biogeographical structure. In fact, a HespDiv method could initially be used to obtain subdivisions, which could then be scrutinised and manually optimised using these additional methods, thereby establishing much more robust and biologically meaningful bioregionalisations.

Comparing Clusters and Subdivision Schemes

One further direction for development is the creation and integration of tools that allow comparisons between identified clusters or entire subdivision schemes. Such comparisons could be approached from three largely independent perspectives: (1) by comparing cluster boundaries, (2) by examining cluster contents (e.g. taxonomic composition), or (3) by assessing global attributes of the subdivision scheme.

The first approach is particularly useful in the context of sensitivity analysis, aimed at assessing the extent to which subdivisions shift spatially when input arguments (e.g. data, subdivision method, criteria) are manipulated. While it might appear that this approach serves primarily to evaluate the reliability of the results, contrasting subdivision outputs from different taxonomic, ecological, or temporal datasets in this manner could yield more fundamental insights. For example, it might reveal how spatial structuring evolves over time or how organisms with different attributes are spatially organised. Currently, subdivision boundaries are compared only through visualisation in a single plot (e.g. Fig. 30). An alternative method for comparing boundaries would be to employ numerical boundary coincidence techniques (see the Boundary Analysis Methods section). Numerical expressions of boundary coincidence could supplement existing visualisation techniques.

The second approach—comparing clusters or subdivision schemes based on their contents—is already used in sensitivity analyses to track how cluster composition changes in response to input argument modifications. However, these comparisons are designed solely to assess cluster stability, as they rely on the direct overlap of occurrence evaluations between clusters. In contrast, comparing the contents of clusters representing different time periods by using various comparison functions could reveal genealogical relationships between geobiomes. If taxonomic HespDiv clusters were explicitly distinguished within spatiotemporal volumes, comparing the contents of adjacent clusters at their temporal boundaries could reveal patterns of genealogical continuity during times of spatial biota transformations. Methods discussed in the Historical Biogeography Methods section could be integrated into the "hespdiv" package to enable more detailed cluster content comparisons, identifying specific biogeographical events, their timing, and the taxa involved.

The third approach entails summarising the features of obtained subdivisions, such as hierarchy depth, overall heterogeneity, the scales at which spatial heterogeneity is most prevalent, and geometrical properties (e.g. size, shape complexity, orientation). It would be illuminating to examine how these features change over time, how they are influenced by various biotic turnover events, and how they depend on organism traits.

Taken together, these three perspectives represent numerous pathways for post-processing HespDiv results and uncovering a diverse array of insights.

3.5.4. Case Studies and Broader Applications

Beyond methodological expansion, HespDiv framework would greatly benefit from additional case studies involving diverse application scenarios. These should not be limited solely to different time periods or organism groups but should also include study designs incorporating consecutive time periods, alternative subdivision approaches, and applications extending beyond bioregionalisation. Systematic comparative studies contrasting HespDiv methods with traditional approaches would also be valuable. Such comparisons could be conducted using both artificial simulated datasets with known properties and real-world data. Particularly illuminating would be investigations in contexts where traditional methods face limitations, but HespDiv methods do not—such as bioregionalisation based on singleton observation datasets. Furthermore, applying HespDiv to abiotic datasets (e.g., geochemical, sedimentological, geomorphological, geological) to reveal entities of other patch-based, nested, dynamic hierarchies would be an exciting avenue of research. Given that HespDiv holds significant potential to resolve spatial instances of Simpson's paradox, applications exploring spatial variation in species distribution models or similar problems would also represent important scientific milestones. Thus, many case studies are still required to fully explore the potential of HespDiv methods.

3.5.5. Summary

The potential of HespDiv methods family is substantial, but much work is needed to explore and fully realise it. The efficiency of the *hespdiv* and *birese* algorithms could be drastically improved with the implementation of parallelisation in steps such as boundary generation, testing, and the subdivision process itself. However, to achieve synchronous subdivision of established clusters, the algorithm structure in *hespdiv* would need to be changed from recursive to iterative. This restructuring would also improve code robustness, making maintenance and development easier.

A radical increase in performance, efficiency and breadth of application could be achieved by changing the way boundaries are generated. An approach based on Thiessen polygon boundaries and Delauny triangulation appears very promising in this regard, though the current *hespdiv* implementation may still hold certain advantages and could be superior in specific scenarios.

As the subdivision patterns revealed by HespDiv methods may often raise more questions than provide answers, future developments should also focus on expanding the range of result post-processing options. Promising directions include methodologies to extract group effects on identified subdivision patterns, evaluate the spatial variability of split-lines, and compare established clusters and entire subdivision schemes, among other avenues.

Finally, many more case studies need to be conducted to fully explore the characteristics of HespDiv methods and uncover the knowledge they can yield.

In conclusion, this thesis lays the groundwork for a substantial research agenda, promising important discoveries and methodological developments that will require years of dedicated research to pursue.

3.6. Summary

The fourth chapter of this thesis has demonstrated the development, implementation, and validation of the HespDiv framework as an innovative approach for detecting and characterising hierarchical structures in spatial and spatiotemporal biological data. This framework, grounded in the conceptual foundations of Bretskyan hierarchy theory, has been shown to address key limitations of existing bioregionalisation and boundary-detection methods.

The *hespdiv* and *birese* methods, developed here, exemplify how the HespDiv family's design allows for flexible, modular, and recursive partitioning of data into hierarchically organised clusters. Notably, *hespdiv* effectively integrates multiple subdivision criteria and methods, supports various input data formats, and allows for both linear and nonlinear boundary constructions. The *birese* method extends this capacity to one-dimensional data, as demonstrated by its application to the Mulde/*lundgreni* event.

Application case studies substantiate the utility and robustness of HespDiv methods. The analysis of Miocene mammalian biogeography across the contiguous United States revealed hierarchical spatial structuring that aligns with known geographical and climatic barriers, while also reflecting previously hypothesised but poorly delineated bioregions. The results underscore the potential of *hespdiv* for uncovering latent spatial structures and providing a probabilistic framework for bioregionalisation.

The application of *birese* to the Mulde/*lundgreni* biotic event in the Gėluva-118 core demonstrated its capacity to identify critical transitions and stages in palaeocommunity dynamics. The findings challenge prior assumptions about the event's duration, revealing a more abrupt and severe extinction-recovery sequence than previously recognised. The quantitative approach applied here, combining high-resolution ostracod data, advanced segmentation, and Bayesian age-depth modelling, exemplifies the power of the HespDiv framework for palaeoecological investigations.

Collectively, these results affirm the potential of the HespDiv framework as a powerful and versatile tool for investigating hierarchical structures in complex biological systems. Its methodological flexibility, coupled with its capacity to generate interpretable, spatially or temporally explicit outputs, provides a solid foundation for future research in biogeography, palaeoecology, and evolutionary biology. Furthermore, the development of accompanying software infrastructure—including the "hespdiv" R package—ensures accessibility, reproducibility, and ongoing methodological refinement.

Future work should focus on extending the HespDiv framework to additional data types and study systems, improving computational efficiency (particularly through parallelisation), and enhancing post-processing capabilities for deeper exploration of subdivision results. Applying these methods across diverse taxonomic groups, temporal scales, and geographic regions will not only test the generality of the framework but also contribute valuable insights into the processes shaping the distribution and structure of life on Earth.

CONCLUSIONS

This thesis presents and develops new approaches in understanding of the hierarchical organisation of the biota across space and time. In the thesis the expansion of the Bretskyan hierarchy theory is presented, transforming it from a conceptual framework into a practical and empirically grounded paradigm for understanding the hierarchical organisation of biota in space and time.

First and foremost, it offers the first empirical operationalisation of Bretskyan units through the development of the HespDiv methodological framework. Its methods—*hespdiv*, *birese*, and post-processing methods within the "hespdiv" package—enables the extraction, characterisation, and sensitivity testing of spatially and temporally contiguous entities consistent with Bretskyan theoretical predictions. These tools allow for the identification of complex, nested geobiomes and their fuzzy boundaries, thereby confirming theoretical expectations and providing a robust basis for future hypothesis testing. Thesis results show that Bretskyan units are not merely conceptual or post-hoc categories. They are detectable features of real-world data, whose properties can be evaluated quantitatively. The application of the developed methods enabled the delineation of three distinct, persistent at the time scale of the Miocene Epoch mammal geobiomes in the contiguous United States—specifically, the West Coast, Central Plains, and Southeast regions. These geobiomes were quantitatively defined for the first time and were found to align closely with known palaeogeographic patterns and established bioregionalisation schemes. Their analysis also confirmed the fuzzy nature of geobiome boundaries, as predicted by Bretskyan hierarchy theory. In addition, analysis of Silurian ostracod assemblages from the Silurian Baltic Basin led to the identification of six nested ostracod-based geobiomes spanning two hierarchical tiers. Specifically, "Old Equilibrium" and "Collapse" geobiomes were nested within a broader "Old Equilibrium + Collapse" unit, which was temporally separated by the "Maximal Stress" phase of the Mulde/*lundgreni* event from a second cluster of geobiomes: "Recovery" and "New Equilibrium," themselves nested within a "Recovery + New Equilibrium" geobiome. This hierarchical structuring illustrates both the temporal dynamics and nesting properties of geobiomes across compositional and environmental transitions. These findings substantiate the central propositions of Bretskyan hierarchy theory and demonstrate its value as a scientific framework.

Second, the thesis provides formal tools to quantify fuzzy boundaries and express their uncertainty, addressing one of the conceptual features of the original theory. By demonstrating that transitions between units are largely probabilistic rather than discrete, this work supports a shift away from traditional categorical bioregionalisation approaches. It enables a more realistic representation of hierarchical structuring, particularly useful for interpreting the nature of large-scale biotic transitions in both space and time.

Third, the integration of the *birese* method with Bayesian age–depth modelling enabled the probabilistic estimation of biotic turnover rates and the temporal delineation of compositional shifts. This combined approach was applied to the Mulde/*lundgreni* event, where it significantly refined the temporal resolution of previously recognised biotic turnover. Specifically, it reduced the estimated duration of the event fourfold, aligning it more closely with macroevolutionary frameworks such as coordinated stasis and punctuated equilibrium. Beyond refining temporal estimates, this analysis also provided the basis for a new, testable hypothesis concerning the internal dynamics of geobiomes: that long-lasting, stable, large-scale geobiomes—such as the "Old Equilibrium" and "New Equilibrium" geobiomes—tend to break down during major environmental perturbations, fragmenting into multiple transient, unstable, and spatially smaller geobiomes—such as those characterised as "Collapse" and "Recovery." This interpretation offers new insight into the structural and temporal dynamics of geobiomes during evolutionary and ecological crises.

Fourth, methodological advancements were consolidated and made accessible to the wider scientific community through the open-source R package "hespdiv" and published *birese* R code as a supplementary material, promoting broad application, transparency, and reproducibility.

Fifth, by reviewing principles of dissipative systems, energy gradients, and cross-scale spatial coupling, the thesis establishes a broader theoretical context that clarifies the nature of biotic and abiotic structuring, leading to the conclusion that such structuring is best understood through hierarchy theory, and more specifically through topologically contiguous hierarchy frameworks such as hierarchical patch dynamics theory and Bretskyan hierarchy theory. This perspective improves our understanding of the emergence and persistence of structural complexity in both biotic and abiotic systems, and predicts the existence of multiple patch-based, dynamic, nested hierarchies topologically analogous to the Bretskyan hierarchy. These findings encourage further exploration of such hierarchies across domains using the conceptual and methodological framework developed herein.

Sixth, in light of this generalisation, the HespDiv methodological family and its methods were developed to maximise flexibility and generality in the subdivision of hierarchical data. These methods enable researchers to analyse a wide range of spatiotemporal data structures and to define custom subdivision logic tailored to the specific traits of their system of interest. This adaptability not only facilitates robust bioregionalisation but also ensures that the framework remains applicable across diverse empirical contexts—from palaeobiological datasets to broader Earth system analyses.

Seventh, this thesis links Bretskyan hierarchy theory with empirical data and common research practices by demonstrating when, how, and with what reliability geobiomes can be reconstructed from palaeobiological records. It makes the formal distinction between empirical, nested, diachronic, compositional Bretskyan-like hierarchies of bioregions, and ontological Bretskyan hierarchy of geobiomes. It further advances the theory by proposing that large-scale geobiomes—particularly those representing distinct habitat types—can spatially overlap, reflecting the complex, multiscale organisation of biotic systems.

In summary, this thesis bridges the gap between Bretskyan theory and empirical application. It validates core theoretical predictions, places the framework within a systems and complexity science context, and introduces powerful, transparent tools for the study of hierarchical structure and dynamics. In doing so, it not only advances Bretskyan theory but also contributes to the broader understanding of how complex systems, especially biotic ones, are structured and evolve across space and time. This thesis transforms the Bretskyan hierarchy theory from a conceptual framework into an empirically testable and broadly applicable paradigm.

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SANTRAUKA

Įvadas

Aktualumas

Disertacijoje nagrinėjama viena iš esminių geobiologijos ir biogeodinamikos problemų – gyvybės įvairovės erdvinė ir laikinė organizacija bei jos pažinimo būdai. Hierarchijos teorija parodė, kad genealoginiai biotos vienetai pasižymi laikinėmis, o ekologiniai – daugiausia erdvinėmis hierarchinėmis struktūromis. Pastaraisiais metais šios įžvalgos buvo apjungtos ir taip pat integruotos su abiotinėmis, geologinių struktūrų hierarchijomis, suformuojant taip vadinamą Bretskio hierarchiją – erdvėlaikinę geobiomų ir holobiontų hierarchinę sistemą (Spiridonov & Eldredge, 2024). Bretskio hierarchijos perspektyvos į gyvybės erdvėlaikinę organizaciją potencialas yra apribotas metodinių būdų aptinki šiuos vienetus analizuojant empirinius paleontologinius duomenis.

Darbo tikslas – sukurti metodinę prieigą ir jos algoritmus, padedančius efektyviai analizuoti hierarchinę biotos erdvėlaikinę organizaciją.

Uždaviniai:

1. Išanalizuoti empirinių ir teorinių tyrimų literatūrą siekiant suprasti biotos erdvinės ir laikinės organizacijos ypatybes bei teorines prieigas, dažniausiai taikomas jai tirti.
2. Apžvelgti biotos erdvėlaikinės hierarchijos tyrimo metodus.
3. Sukurti efektyvią metodinę prieigą, tiesiogiai suderintą su Bretskio hierarchijos teorija.
4. Išvystyti skaičiavimo algoritmus pagal šią metodinę prieigą.
5. Integruoti šiuos metodus į plačiai prieinamą atvirojo kodo statistinių skaičiavimų platformą R kaip paketą.
6. Patikrinti prieigos efektyvumą empirinių duomenų pagrindu, pritaikant metodus mioceno ir silūro biotos erdvinės ir laikinės hierarchinės organizacijos tyrimams.

Naujumas ir reikšmė.

Siekiant apibrėžti Bretskio hierarchijos teorijos vienetus empiriniuose duomenyse, sukurta nauja metodinė prieiga – HespDiv metodų šeima, apimanti du metodus (*hespdiv* ir *biresе*), įdiegtus naujai sukurtame „hespdiv“ R pakete. Šiame darbe *hespdiv* metodas pritaikytas siekiant atskleisti mioceno žinduolių geobiomus ir jų stabilumą JAV teritorijoje (Daumantas & Spiridonov, 2024b). Tuo tarpu *birese* metodas buvo pritaikytas Silūro ostrakodų gausumo duomenims iš Gėluva-118 gręžinio intervalo apimančio Mulde/*lundgreni* biotinį įvykį (Rinkevičiūtė et al., 2025). Šiame tyrime pasitelkiant *birese*, pavyko nustatyti ir patikslinti Mulde/*lundgreni* įvykio trukmę, ostrakodų bendrijų dinamiką įvykio intervale bei identifikuoti pagrindinius ostrakodų geobiomus.

Metodų pritaikymo atvejai atskleidė, buvo sukurta prieiga yra efektyvi ir padeda automatiškai identifikuoti Bretskio hierarchijos vienetus iš empirinių duomenų. Tai naujas ir kol kas vienintelis būdas atpažinti ir analizuoti šios naujai sukurtos ir kol kas mažai pažintos gyvybės erdvėlaikinės hierarchijos teorijos vienetus. Kita vertus, disertacijos rezultatai praplėtojo Bretskio hierarchijos teoriją. HespDiv šeimos metodų taikomieji tyrimai parodė, kad Bretksio hierarchijos vienetai – ne tik teoriniai, bet ir praktiškai atpažįstami empiriniuose fosilijų duomenyse. Gauti rezultatai atskleidė naujus geobiomų bruožus (pvz., intrakontinentinių JAV mioceno žinduolių biogeomų ribų blausumą ir tikimybinę tokių geobiomų prigimtį). Taip pat jie patikslino Mulde/*lundgreni* įvykio trukmę ir eigą. Taigi, HespDiv metodai suteikia naujas galimybes tyrinėti biotos erdvėlaikinę organizaciją, sumažina biogeografinių regionalizacijų subjektyvumą ir suteikia Bretskio hierarchijos teorijai empirinį pagrindimą.

Pagrindinės tezės:

- HespDiv yra efektyvi, nauja, pamatinė ir plati metodologinė prieiga, tinkanti Bretskio hierarchijos vienetų analizei ir sudaranti naują metodų šeimą
- Sukurti HespDiv metodai (*hespdiv* ir *birese*) ne tik padeda identifikuoti Bretskio hierarchijos vienetus, bet leidžia įgyti naujų empirinių įžvalgų į erdvėlaikinę biotos dinamiką.

1. Laikinė ir Erdvinė Gyvybės Organizacija Žemėje

Šioje disertacijos dalyje siekiant įgyvendinti pirmąją disertacijos užduotį apžvelgti gyvybės erdvėlaikinės organizacijos principai ir teorinės prieigos naudojamos ją paaiškinti. Prieita prie išvados, kad Bretskio hierarchija yra perspektyviausia teorinė prieiga aiškinant biotos erdvėlaikinę hierarchinę organizaciją Žemėje.

1.1. Struktūrinis Sudėtingumas Gamtoje

Šiame skyriuje apžvelgti universalūs termodinamikos, sistemų teorijos, hierarchijų teorijos ir sudėtingumo mokslo (angl. *complexity science*) principai, kurie veikia tiek biotos, tiek abiotos erdvėlaikinę organizaciją. Šios apžvalgos pagrindinė idėja ta, kad erdvinio susietumo (pvz., gretimumo ar persidengimo) įgalintos fizinių esinių ir energijos gradientų sąveikos lemia erdvėlaikyje lokalizuoto kintamumo kaskadas. Šios kaskados gali būti tiek generuojančios (kuriančios naujus esinius ir gradientus), tiek griaunančios (naikinančios esamus). Jų palaikymui itin svarbios disipacinės sistemos (Prigogine, 1984). Disipacinės sistemos veikia toli nuo pusiausvyros, yra atviros ir jų struktūrą palaiko energijos šaltiniai, kurių energiją jos disipuoja (sklaido) – pavyzdžiui, žvaigždžių vidinę dinaminę struktūrą ir vykdomą spinduliuotę palaiko branduolinė sintezė, kuri yra gravitacinio kolapso ir su juo susijusių gravitacinių potencialų gradientų pasekmė. Disipacinių sistemų svarba kintamumo kaskadoms pasireiškia tuo, kad jų energijos gradientai gali dalyvauti sąveikose su kitais esiniais ir gradientais – pvz. Saulės spinduliuotė lemia ir palaiko atmosferos bei hidrosferos cirkuliaciją Žemėje. Aprašyta kintamumo kaskadų prigimtis bei varijuojanti ir nuo mastelio priklausanti sukurtų darinių gyvavimo trukmė lemia netolygų, heterogenišką bei hierarchišką fizinių esinių ir energijos gradientų įvairovės pasiskirstymą tiek laike, tiek erdvėje (Chaisson, 2001). Tokį fizinių esinių pasiskirstymą gana gerai apibūdina hierarchinė lopų dinamikos (angl. patch hierarchy dynamics) teorija pasiūlyta kraštovaizdžio ekologijos kontekste (Wu & Loucks, 1995), ypač jei ją generalizuojame už ekologijos mokslo ribų. Vienas svarbiausių jos bruožų yra topologinė struktūra – ją sudarantys esiniai erdvėje ir laike yra vientisi.

1.2. Hierarchijų Teorija

Atsižvelgiant į aptartą hierarchinių struktūrų paplitimą tiek gyvojoje, tiek negyvojoje gamtoje, šiame skyriuje apžvelgta hierarchijų teorijos mokslo esminiai bruožai, istorija, hierarchijos koncepcija, pagrindiniai hierarchijų elementai bei jų sudarymo principai ir hierarchijų teorijos apribojimai. Taip pat buvo apžvelgta hierarchijų teorijų įvairiose mokslo srityse įvairovė. Apžvelgiant hierarchinių lygmenų išskyrimo principus, iškelta hipotezė bei pateiktas argumentavimas, kad sunkiausiai pažįstami hierarchijų lygmenys yra aukščiausio rango. Nagrinėjant hierarchijų teorijos mokslo trūkumus atkreiptas dėmesys, kad hierarchijų teorijos dažnai konstruojamos taip, kad sutaptų su mokslo sričių ribomis (Spiridonov & Eldredge, 2024). Tokiu būdu gautos hierarchijos dažnai apima tuos pačius esinius suteikdamos ribotą perspektyvą į juos (pvz. koralai svarbūs tyrimo objektai tiek ekologijos, tiek evoliucijos, tiek geologijos moksluose). Dėl to siekiant vertinti biotinius esinius platesniame kontekste tenka naudoti ne vieną hierarchijų teoriją (pvz. dualistinė hierarchinė prieiga regi biotinius esinius kaip priklausančius persipynusioms ekologinei ir genealoginei procesų hierarchijoms (Eldredge, 1985; Eldredge & Salthe, 1984)). Tačiau tokia prieiga jau gali būti kritikuojama kaip pernelyg sudėtinga ir griozdiška praktiniam taikymui (Gould, 2002; Rosenberg, 2022). Kaip atsakas į šiuos hierarchijų teorijos taikymo biotai trūkumus neseniai buvo sukurta Bretskio hierarchijos teorija (Spiridonov & Eldredge, 2024). Ji ne tik kad apima ekologinius ir genealoginius procesus, bet ir yra smarkiai integruota su abiotinio pasaulio procesais, kontroliuojančiais gyvybės erdvinę fragmentaciją. Dėl šių priežasčių Bretskio hierarchijos teorija buvo pasirinkta kaip tinkamiausia teorinė paradigma šiai disertacijai. Taigi, sukurta metodika buvo vertinta ir lyginta su kitais metodais pagal jos tinkamumą atskleisti ir analizuoti Bretskio hierarchijos vienetus.

1.3. Bretskio Hierarchijos Teorija

Bretskio hierarchijos teorija pristatyta Spiridonov and Eldredge (2024). Šiame skyriuje pateiktas jos apibrėžimas, aptarti jos esiniai, sąsajos su negyvąja gamta, pateikti Bretskio hierarchijos pavyzdžiai bei apgalvoti Bretskio hierarchijos taikymo empiriniams duomenims ypatumai. Bretskio hierarchijos teorija yra hibridinė hierarchijos teorija gauta apjungus ekologinę bendrijų, ekosistemos ir genealogijos hierarchijas. Kiekvienos šių hierarchijų eisminis bruožas yra integruotas Bretskio hierarchijoje, atitinkamai: biotinės sąveikos, gyvosios ir negyvosios gamtos sąveikos bei genealoginės informacijos perdavimas. Teorija pavadinta pagal Peter‘į Bretsk‘į, amerikietį paleontologą, dėl to, kad jis atkreipė dėmesį į diskretų biotos pasiskirstymą erdvėlaikyje (Eldredge, 1985). Bretskio hierarchijos esiniai yra biotinės sistemos, kurių erdvines ir laikines ribas apibrėžia vidinė energijos, medžiagų ir informacijos pernaša. Šios sistemos sudarytos iš biotinių individų populiacijų (pvz. bendrijų). Teorija numato du esinių tipus: holobiontus ir geobiomus. Holobiontai yra mažos sistemos, sudarytos iš funkciniais ryšiais stipriai integruotų biotinių individų. Geobiomai yra kur kas didesnės sistemos, sudarytos iš polifiletinių biotinių individų populiacijų, kurių ekologinė integracija yra kur kas silpnesnė nei holobiontų (geobiomuose dominuoja sąveikos tarp gyvosios ir negyvosios gamtos, o ekologinė integracija pasireiškia per įvairias ekologines sąveikas bei koevoliuciją) ir įgalinta dėl gyvenimo toje pačioje geografinėje erdvėje – kohabitacijos, kurią lemia daugelio rūšių paplitimą ribojantys biogeografinių barjeriai. Tiek holobiontai, tiek geobiomai turi genealoginę reikšmę – jie pasižymi skirtingu prisitaikymu, turi pradžią ir pabaigą laike bei gali turėti palikuonių, kuriems perduoda savo savybes. Geobiomų reprodukcija yra sąlygota jų skilimų ir susiliejimų, kurie savo ruožtu susiję su biogeografinių barjerų dinamika, o pastaroji su geodinamika. Dėl tokio reprodukcijos pobūdžio geobiomų hierarchijos topologija primena klaidžiojančius srautus, kuriuose vagos gali tiek susilieti, tiek atsiskirti. Kita svarbi geobiomų ir holobiontų topologinė savybė yra erdvinis ir laikinis vientisumas.

Kadangi Bretskio hierarchijos teorija yra šios disertacijos paradigma, disertacijos perfrazuotas tikslas yra „sukurti metodinę prieigą ir algoritmus efektyviai geobiomų hierarchinės organizacijos analizei". Bretskio hierarchijos savybės lemia būtinąsias metodikos savybes: (1) metodo išvestis turi būti hierarchiškai organizuota, (2) išskirti hierarchijos vienetai turi būti vientisi tiek erdvėje, tiek ir laike; vientisumas erdvėje reiškia, kad ribos erdvėje turi būti vientisos ir uždaros (ribos pradžia susijungia su galu), (3) ribos tarp hierarchijos vienetų turi sutapti su nevientisumais materijos, energijos ir informacijos biotinėje pernašoje. Norint užtikrinti pastarąją savybę pagrindiniai stebėjimai, kurių pagrindu turėtų veikti metodika atskleisdama geobiomų hierarchiją, turėtų būti taksonominiai gausumo arba aptikimų duomenys. Pagrindė dėl to, nes taksonominė informacija atspindi genealoginius procesus ir šių procesų atskyrimas erdvėje turėtų sukurti erdvėlaikyje diskrečias taksonomines fosilijų asociacijas.

Pagrindinė Bretskio hierarchijos empirinio atskleidimo problema yra paleontologinio metraščio fragmentiškumas ir jo heterogeniškas pasiskirstymas laike ir erdvėje (Antell et al., 2024; Patzkowsky & Holland, 2012; Peters & Heim, 2010; Wagner & Marcot, 2013). Dėl šių priežasčių bei dėl to, kad tipiškai tyrimai apsiriboja tam tikromis taksonominėmis grupėmis vietoj to, kad apimtų visą biotą, iš empirinių taksonominių gausumo ar aptikimo duomenų aptikta geobiomų hierarchija net naudojant idealius metodus iš esmės turėtų skirtis nuo ontologinės Bretskio hierarchijos. Šie skirtumai yra pakankamai reikšmingi, kad empiriškai, taksonominių duomenų pagrindu išskirtas hierarchijas, kurios turi Bretskio hierarchijos topologinę struktūrą, nereikėtų laikyti Bretskio hierarchijomis. Šiame skyriuje joms suteiktas pavadinimas yra Bretskiškos hierarchijos (angl. Bretskyan-like hierarchies). Tikroji Bretskio hierarchijos geobiomų organizacijos struktūra turėtų būti Bretskiškosios hierarchijos interpretacijos rezultatas ir idealiu atveju turėtų būti patvirtinta nepriklausomais būdais.

2. Metodai Naudojami Biotos Erdvėlaikinės Organizacijos Tyrimuose

Šioje disertacijos dalyje, siekiant įgyvendinti antrąją disertacijos užduotį, atlikta metodų, naudojamų tyrinėti biotos erdvėlaikinę organizaciją, apžvalga. Apžvelgtos trys stambios metodų grupės: bioregionalizacijos metodai, ribų metodai, istorinės biogeografinės metodai. Įvertintas šių metodų tinkamumas atskleisti ir analizuoti Bretskio hierarchiją. Prieita prie išvados, kad kol kas nėra metodo pritaikyto efektyviems Bretskio hierarchijos atskleidimo tyrimams.

2.1. Bioregionų aptikimo ir analizės metodai

Populiariausi bioregionalizacijos metodai yra veikia klasterinės analizė, ordinacijos analizė ir tinklų analizė (pav. 4). Kur kas rečiau bioregionalizacijoje pasitelkiami ir endeminių zonų aptikimo metodai: parsimoninė endmiškumo analizė (Brian R. Rosen, 1988), endemiškumo analizė (Szumik et al., 2002) bei biotinių elementų analizė (Hausdorf & Hennig, 2003). Taip pat yra eilė metodų skirtų išskirtų bioregionų *post-hoc* analizėms, tokie kaip ANOSIM, kuris įvertina bioregionalizacijos statistinį reikšmingumą (Clarke, 1993), SIMPER, kuris atlieka skirtumų tarp bioregionų taksonominę dekompoziją (Clarke, 1993) ar IndVal (Dufrene & Legendre, 1997), kuris leidžia identifikuoti bioregionus labiausiai išskiriančius taksonus.

Visi apžvelgti bioregionalizaciniai metodai turi ribotą tinkamumą atskleisti ir analizuoti Bretskio hierarchiją. Visų pirma, ne visi užtikrina hierarchinę išvesties struktūrą, erdvėlaikinį bioregionų vientisumą ar apskritai bioregionų ribų buvimą išvestyje. Antra, šie metodai įvestyje reikalauja skirtumų/atstumų matricos. Šiame skyriuje buvo pademonstruota, kad jeigu duomenyse dominuoja geografiniai singletonai (vietovės su vienu aptikimu), tuomet skirtingų ekologinių metrikų taikymas gauti skirtumų/atstumų matricas konverguoja į vienintelę įmanomą išvestį, nepriklausomai nuo pasirinktos metrikos. Kitaip tariant, ekologinės metrikos pasirinkimas, nors turėtų suteikti skirtingas perspektyvas į duomenis, tokiais atvejais tampa nebesvarbus rezultatui. Tikėtina, kad kai aptikimų skaičius per vietovę artėja link vieneto, skirtingų ekologinių metrikų skirtumai tarp vietovių taksonomijos panašėja. Kadangi, vietovės su maža rušių įvairove paprastai dominuoja makroekologiniuose duomenyse (Brown, 1995), tai gali būti platesnė problema. Trečia, bioregionų taksonominiai skirtumai išreikšti per skirtumų/atstumų matricas yra kitokie nei pamatuoti tiesiogiai taikant tas pačias metrikas. Dėl šių priežasčių klasterinės, ordinacijos ir tinklų analizės rezultatai yra sunkiau interpretuojami.

2.2. Ribų Analizės Metodai

Apžvelgti du metodai naudojami ieškant 0D, 1D arba 2D ribų: skelto slenkančio lango metodas (Webster, 1978) ir wombling‘as (Womble, 1951). Pirmasis metodas leidžia aptiki 0D ribas 1D duomenyse, o antrasis – 1D arba 2D ribas geografiniuose arba erdvėlaikiniuose duomenyse. Taip pat apžvelgti gautų ribų analizės metodai, atskleidžiantys ribų plotį, storį, mastelį, persidengimą su kitomis ribomis bei statistinį reikšmingumą.

Ribų išskyrimo metodai turi ribotą pritaikomumą pilnavertei Bretskio hierarchijos analizei, kadangi aptiktos ribos nėra uždaros, tad ne visada įmanoma identifikuoti erdvėje vientisus bioregionus, jau nekalbant apie jų hierarchinės struktūros atskleidimą.

2.3. Istorinės Biogeografijos Metodai

Istorinės biogeografijos metodai padeda atskleisti taksonų geografinio paplitimo istorinę raidą, biogeografinius įvykius ir lokalizuoti erdvėje ir laike makroevoliucinius įvykius, t.y. rūšių atsiradimo ir išnykimo vietas. Skyriaus pradžioje apžvelgti istorinės reikšmės metodai: dispersalizmas (Morrone & Crisci, 1995), filogenetinė biogeografija (Morrone, 2023), panbiogeografija (Morrone, 2015) bei kladistinė biogeografija (Lundberg, 1993). Prie šių metodų taip pat galima priskirti ir parsimoninę endemiškumo analizę, kuri buvo apžvelgta prie bioregionalizacijos metodų. Antroje skyriaus pusėje apžvelgti naujieji, populiarūs istorinės biogeografijos metodai: dispersijos-vikariancijos analizė (angl. Dispersal-Vicariance Analisis, DIVA) (Ronquist, 1997), dispersijos-išmirimo-kladogenezės modelis (angl. Dispersal-Extinction-Cladogenesis, DEC) (Ree et al., 2005; Ree & Smith, 2008) bei BioGeoBEARS metodas (Matzke, 2013; Matzke, 2014; Matzke, 2018). Metodai gebantys atskleisti Bretskio hierarchijos vienetus turėtų puikiai integruotis su istorinės biogeografijos metodais, kadangi pastarieji įvestyje reikalauja apibrėžtų teritorinių vienetų. Šiais vienetais galėtų būti atskleisti geobiomai. Ši apžvalga atskleidė, kad nors istorinės biogeografijos metodai netinkami aptikti geobiomų ir atskleisti jų hierarchinę organizaciją, jie puikiai tiktų juos analizuoti ir suprasti atskirų taksonų vaidmenį geobiomų istorinėje raidoje bei išplitimo barjerų, skiriančių geobiomus, prigimtį.

3. HespDiv Prieiga

Ši disertacijos dalis pristato pagrindinius 3-6 disertacijos užduočių atlikimo rezultatus ir yra pagrindinė disertacijos dalis. Joje pristatoma hierarchinė erdvinių duomenų suskaidymo prieiga, HespDiV metodų šeima (**hie**rarchical **sp**atial **d**ata sub**div**ision, HespDiv), du šios šeimos metodai ir jų algoritmai, R paketas „hespdiv“, kuriame yra integruoti šie algoritmai bei jų rezultatų *post-hoc* analizės metodai. Sukurtų metodų efektyvumas išbandytas dviejuose paleontologinių duomenų tyrimuose. Gauti rezultatai publikuoti dviejuose šios disertacijos temos straipsniuose (Daumantas & Spiridonov, 2024b; Rinkevičiūtė et al., 2025) ir taip pat yra pristatyti šioje disertacijos dalyje. Papildomai šiame skyriuje apžvelgtas sukurtų metodų tinkamumas empiriniams Bretskio hierarchijos atskleidimo ir analizės tyrimams, taip pat sukurti metodai pagal savo tinkamumą lyginti su kitais apžvelgtais metodais (lentelė 2). Galiausiai apžvelgtos HespDiv metodų šeimos ateities perspektyvos ir numatyta tolimesnių tyrimų programa.

3.1. HespDiv Metodų Šeimos Savybės

HespDiv šeimos metodai pasižymi tokiomis penkiomis savybėmis:

1. Naudodamas erdvėje, laike ar erdvėlaikyje apibrėžtas ribas metodas rekursyviai dalija įvesties duomenis į du erdvėje vientisus poaibius, taip organizuodamas juos į hierarchinę struktūrą. Šioje struktūroje kiekvienas aukštesnio hierarchinio lygmens padalinimas yra griežtas žemesniojo hierarchinio lygmens padalinimo poaibis.
2. Pagrindinė metodo įvestis – palyginimo funkcija, kuri nustato, kaip duomenų aibės sulyginamos. Ši funkcija priima du duomenų poaibius atskirtus laikine, erdvine arba erdvėlaikine riba ir išvestyje pateikia sulyginimo vertę (pvz. skirtumą, panašumą ar kokią kitą metriką). Ji lemia ribų kokybės vertinimą ir atranką bei tai, kokius duomenų tipus metodas gali apdoroti. Dėl modulinio dizaino HespDiv metodai yra itin lankstūs: gali būti pritaikomi įvairioms duomenų struktūroms, duomenų tipams bei duomenų skaidymo strategijoms.
3. Metodas kiekvienoje rekursijoje dinamiškai koreguoja savo mastelį ir laikinę, erdvinę ar erdvėlaikinę aprėptį. Ši savybė užtikrina, kad gauti padalinimai turi savo būdingąjį mastelį susietą su konkrečiu

hierarchiniu lygmeniu – pvz., aukštesnio rango padalinimai aptinka mažesnius, žemesnio rango Bretskiškosios hierarchijos geobiomus.

4. Rezultatai išreiškiami 0D, 1D ar 2D ribomis, atskiriančiomis laikinius ar erdvinius segmentus, erdvinius plotus, ar erdvėlaikinio tūrinius kūnus. Šios ribos kartu su jų hierarchine struktūra ir priskirtomis palyginimo reikšmėmis sudaro pagrindinį metodo išvestį. Ribų dimensijos, jų generavimo ir optimizavimo algoritmai priklauso nuo konkretaus HespDiv metodo.
5. Ribos apibrėžia dvi papildomas hierarchiškai organizuotas išvestis: HespDiv klasterius (duomenų poaibius išvisų pusių apsuptus duoto hierarchinio rango ribomis) ir jų erdvinius, laikinius ar erdvėlaikinius domenus (laiko, erdvės ar erdvėlaikio dalis apibrėžtas tomis pačiomis ribomis).

3.2. HespDiv Metodai

Sukurti du HespDiv metodai: *hespdiv* ir *birese.* Abu HespDiv metodai pasižymi panašia eiga:

1. Padalinimų generavimas.
2. Padalinimų testavimas naudojant palyginimo funkciją ir geriausio padalinimo atranka ir panaudojimas įgyvendinant duomenų atskyrimą.
3. 1-2 žingsnio kartojimas tol kol leidžia duomenų skaidymo sustabdymo kriterijai.

3.2.1. *hespdiv*

Pirmasis HespDiv metodas sukurtas disertacijos eigoje yra *hespdiv*. Jis pristatytas (Daumantas & Spiridonov, 2024b). Metodo tikslas – hierarchiškai suskaidyti duomenis erdvėje tiesiniais arba netiesiniais padalinimais, kurie optimizuoja palyginimo funkcijos išvestį. Metodo įvestis: (1) duomenys (duomenų prigimtis, tipas ir struktūra gali būti įvairi) bei jų koordinatės (pateikiami duomenų lentelėje arba matricoje), (2) palyginimo funkcija (kartu galima pateikti duomenų generalizavimo funkcija, kuria būtų apdorojami duomenys prieš juos pateikiant palyginimo funkcijai), (3) įvairūs duomenų skaidymo sustabdymo kriterijai, tokie kaip minimalus poligono plotas, minimalus vietovių skaičius, minimalus stebėjimų skaičius, maksimalus leistinas poligonų dydžių, vietovių skaičiaus ir stebėjimų skaičiaus santykinis skirtumas. Kiti metodo parametrai kontroliuoja padalinimų optimizavimo algoritmą bei padalinimų generavimą (padalinimų skaičių, padalinimų tankio arba skaičiaus per poligoną pastovumą, ir padalinimų geometriją – tiesiniai ar netiesiniai, ir jei netiesiniai, tai kiek leidžiama varijuoti formai). Metodo algoritmo detali eiga yra pavaizduota Pav. 25.

Ribų generavimas

Ribos generuojamos ant skaidomo poligono perimetro reguliariais tarpais išdėstant taškus ir juos sujungiant Kartezinėje geografinių koordinačių plokštumoje tiesiomis linijomis. Perimetro taškų skaičius yra viena iš metodo įvesčių, kuri lemia sugeneruotų padalinimų skaičių ir analizės detalumą (jei n yra perimetrų taškų skaičius, tai padalinimų skaičius yra $\frac{n(n-1)}{2}$). Kitas parametras kontroliuoja ar išlaikyti pastovų perimetro taškų skaičių (numatytasis veikimas), ar pastovų atstumą tarp perimetro taškų.

Taip pat yra opcija generuoti padalinimus, kurie nėra tiesiniai Kartezinėje plokštumoje (tai numatytasis veikimas). Tokiu atveju pirmiausia vis tiek yra generuojami jau aprašyti tiesiniai padalinimai, tarp jų nustatomas optimaliausias ir tada šis tiesinis padalinimas yra naudojamas kaip pagrindas kurti netiesiniams padalinimams. Netiesiniai padalinimai kuriami kaip matematiniai, kubiniai splainai. Splainai yra tolydžios kreivės, suvaržytos glotniai interpoliuoti per duotus taškus, taip vadinamus mazgus. Mazgų išdėstymas lemia kreivės formą (Pav. 25, žingsnis 4). Mazgai yra išdėstomi stulpeliais, kurie ortogonalūs optimaliausiam tiesiniam padalinimui. Parametrais galima kontroliuoti mazgų skaičių stulpelyje (numatyta reikšmė 10) ir kiek stulpelių reguliariais tarpais turi būti išdėstyta išilgai tiesinio padalinimo (numatyta reikšmė 5). Stulpelių skaičius lemia kiek padalinimas gali turėti vingių, o mazgų skaičius stulpelyje – kiek skirtingų formų kiekvienas vingis gali įgyti. Generuojant netiesinius padalinimus, splainams sukurti yra naudojamos skirtingos mazgų iš kiekvieno stulpelio kombinacijos.

Ribų testavimas

Ribos, tiek tiesinės, tiek netiesinės, testuojamos šiais žingsniais:

1. Sugeneruota riba yra pritaikoma padalinti poligoną į dvi dalis, o duomenis į du poaibius.

2. Patikrinami skaidymo sustabdimo kriterijai: stebėjimų ir vietovių kiekis kiekviename poligone, polygonų dydžiai, bei šių kiekių ir dydžių santykiniai skirtumai.
3. Jei kriterijai patenkinami, kiekvienam duomenų poaibiui pritaikoma generalizavimo funkcija (numatytoji funkcija grąžina įvestį), o tada duomenų palyginimo funkciją. Šios išvestis leidžia įvertinti padalinimo kokybę ir identifikuoti optimaliausią padalinimą.

Metode, kuris integruotas „hespdiv“ R pakete, dėl patogesnio naudojimo yra įdiegtos keturios išankstinės skirtingos generalizacijos ir palyginimo funkcijų kombinacijos, leidžiančios atlikti bioregionalizaciją keturių ekologinių panašumo metrikų pagrindu: Jaccard‘o, Sorensen‘o-Dice‘o, Morisita bei Morisita-Horn. Numatytasis metodas – Morisita-Horn. Visų šių metodų numatyta duomenų įvestis yra fosilijų aptikimų taksonominių vardų vektorius.

Išvestis ir jos Analizė: „hespdiv“ paketo infrastruktūra

R paketas „hespdiv“ yra atviro kodo ir apima *hespdiv* metodo algoritmo funkciją bei jos išvesties analizės metodus. Paketas yra aktyviai vystomas toliau, pridedant naujų *post-hoc* analizės ir vizualizacijos opcijų, taip pat numatyta sukurti ir integruoti naujų HespDiv šeimos metodų. Dabar pakete galima rasti funkcijų, kurios (1) naudodamos duomenų permutacijos principu veikiančius nulinius modelius patestuoja padalinimų statistinį reikšmingumą, (2) įvairiais būdais vizualizuoja gautų padalinimų ir poligonų hierarchiją (2D, 3D dendrogramos ir žemėlapiai), (3) įvairios jautrumo analizės funkcijos, leidžiančios įvairiai patikrinti gautų ribų ir HespDiv klasterių stabilumą pokyčiams *hespdiv* parametruose (pvz. imties pokyčiams, palyginimo funkcijai, duomenų skaidymo sustabdymo kriterijams), (4) inovatyviais metodais įvertina taksonų arba taksonominių grupių įtaką kiekvienam padalinimui ir visai bioregionalizacijai (ruošiama publikacija).

Instaliavus įrankių rinkinį RTools, naujausia paketo versija gali būti instaliuota R aplinkoje tiesiogiai iš GitHub su šiuo šaukiniu (palaikoma R versija >= 4.0):

```
if (!require("devtools")) install.packages("devtools")
devtools::install_github("Liudas-Dau/hespdiv", ref = "newfeatures")
```

3.2.2. *birese*

Metodas *birese* (**bi**narinė **re**kursyvi **se**gmentacija, angl. **bi**nary **re**cursive **se**gmentation) ir jo kodas pristatytas antroje disertacijos publikacijoje (Rinkevičiūtė et al., 2025). Šis metodas skirtas vienadimensinių duomenų (erdvinių ar laikinių eilučių) rekursyviam binariniam suskaidymui į hierarchiškai organizuotus segmentus. Skaidymas atliekamas analogišku principu *hespdiv* metodui:

1. Sugeneruojamos 0D ribos – padalinimo taškai. Šie taškai pridedami vidurinėse padėtyse tarp gretimų stebėjimų. Kitaip nei *hespdiv* ribos, tokios *birese* ribos leidžia ištestuoti visus įmanomus duomenų eilutės padalinimus.
2. Taškai panaudojami atskirti duomenis į du laiko ar erdvės eilutės segmentus – vienas iki taško, kitas anapus taško.
3. Patestuojama ar duomenų kiekis segmentuose yra pakankamas (tai vienintelis segmentavimo sustabdymo kriterijus).
4. Jei pakankamas, dviejų segmentų duomenys yra palyginami naudojant įvestyje pateiktą palyginimo funkciją.
5. Optimaliausias padalinimo taškas yra panaudojamas įtvirtinti padalinimui, o gauti du segmentai yra toliau segmentuojami tuo pačiu principu pagal 1-5 žingsnius, tol kol leidžia segmentavimo sustabdymo kriterijus.

Gauta segmentų hierarchinė organizacija vizualizuojama laiko arba erdvės eilutėje atvaizduojant gautus segmentus stačiakampiais. Žemesnio rango segmentų stačiakampiai yra perdengti aukštesnio rango segmentų stačiakampiais. Stačiakampio aukštis atspindi padalinimo kokybę. Iš stačiakampių gautos struktūros tokioje vizualizacijoje primena bokštus, piramides, terasinius slėnius, platformas ar kitokius darinius. Šie dariniai atspindi duomenų hierarchinės organizacijos laiko ar erdvės eilutėje ypatumus, tad yra kritiškai svarbūs interpretacijoje (Rinkevičiūtė et al., 2025).

3.3. Atvejų tyrimai

Disertacijoje pristatyti du taikomieji HespDiv metodų atvejų tyrimai: mioceno žinduolių bioregionalizacijos tyrimas ir Mulde/*lundgreni* biotinio įvykio trukmės ir biotinės struktūros tyrimas.

3.3.1. Mioceno Žinduolių Biogeografija

Sukurtas *hespdiv* metodas buvo pritaikytas atskleidžiant mioceno žinduolių biogeografija Jungtinių Amerikos Valstijų (JAV) teritorijoje (Daumantas & Spiridonov, 2024b). Tyrimo tikslas buvo patestuoti bei pristatyti metodą ir jo gebą atskleisti Bretskio hierarchiją. Tyrime atskleista hierarchinė Bretskiška organizacija dera su ankstesnių mioceno žinduolių biogeografinių tyrimų rezultatais ir žinomais geografiniais barjerais JAV. Trys savo patikimumu ir reikšme išskiriantys bioregionai interpretuoti kaip geobiomai. Taigi, tai pirmas kartas istorijoje, kai Bretskio teorijai buvo suteiktas empirinis pagrindas ir su tam skirtais metodais identifikuoti potencialūs Bretskio hierarchijos vienetai.

Duomenys

Tyrime naudoti neskraidančių sausumos žinduolių aptikimų JAV teritorijoje duomenys iš paleontologinių duomenų bazės (https://paleobiodb.org).

Metodai

Šiems duomenims buvo pritaikytas *hespdiv* metodo funkcija *hespdiv()* su numatytomis parametrų vertėmis bei 75 padalinimų taškais.

Padalinimų statistinis reikšmingumas vertintas su *nulltest()* funkcija, kuri Monte Karlo permutacijos metodu sugeneruoja nulinį padalinimo kokybės pasiskirstymą, atspindintį, kokia būtų padalinimų kokybė, jei aptikimai po fosilijų radimvietes būtų pasiskirstę atsitiktinai, tai yra be jokios biogeografinės tvarkos.

Rezultatams taip pat pritaikyta jautrumo analizė imties sudėčiai. Tai buvo daroma kartojant *hespdiv* bioregionalizaciją 100 kartų su vis kita 80 % duomenų imtimi pasitelkiant *hsa()* funkciją. Šių rezultatų pagrindu buvo vertintas ribų ir klasterių stabilumas. Ribų stabilumas buvo vertinamas vizualiai, su *plot_hsa()* funkcija atvaizdavus visus gautus to paties rango padalinimus viename grafike. Klasterių stabilumas buvo vertinamas kiekybiškai, su *hsa_quant()* funkcija matuojant, kiek klasterių stebėjimų sudėtis (t.y., aptikimų indeksų aibės) pagal Jaccard‘o metrika persidengia su klasteriais gautais alternatyviose jautrumo analizės bioregionalizacijose. Aukščiausių persidengimo verčių (t.y. tos kurios atitinka persidengimą su analogišku / panašiausiu klasteriu alternatyvioje bioregionalizacijoje) empiriniai tikimybės tankio funkcijų grafikai vizualizuoti su *plot_hsa_q()* funkcija.

Rezultatai

Rezultatuose gauta 14 padalinimų, kurie sukūrė 29 *hespdiv* poligonų erdvinę hierarchinę 7 lygmenų dendrogramą (pav. 27, 29, papildomos medžiagos 1 pav.). 11 padalinimų buvo statistiškai reikšmingi (Pav. 28). Jautrumo analizės atskleidė, kad pirmo ir antro rango padalinimai buvo itin stabilūs duomenų variacijoms (pav. 30). Šie padalinimai taip pat buvo statistiškai reikšmingi ir apibrėžė tris didžiausius ir hierarchiškai reikšmingiausius *hespdiv* bioregionus (Pietryčių JAV, Vakarų Pakrantė, Centrinės Lygumos), kurie taip pat pasižymėjo ir stabiliais klasteriais (pav. 31). Trečio-penkto rango padalinimų stabilumas buvo mažesnis, bet pakankamai išreikštas, kad šių padalinimų fragmentai būtų pastebimi alternatyviose bioregionalizacijose (pav. 30). Tuo tarpu šešto-septinto rango padalinimai nebuvo stabilūs. Aukštesnio rango padalinimai apskritai pasižymėjo sudėtingesne bioregionų geometrija, mažesniu statistiniu reikšmingumu ir prastesne kokybe (aukštesnėmis panašumo vertėmis) (pav. 32, 29). Didžioji dalis išskirtų *hespdiv* klasterių (19 iš 28) buvo stabilūs, penki klasteriai klasifikuoti kaip nestabilūs, keturi iš dalies stabilūs (pav. 31). Taip pat stebėta, kad Centrinės Lygumos bioregionas, esantis JAV centrinėje dalyje, pasižymėjo silpniausiais vidiniais padalinimais, lyginant su kitais dviem reikšmingiausiais bioregionais (pav. 27).

Diskusija

Pietryčių JAV, Centrinių Lygumų ir Vakarų pakrantės bioregionai dėl statistinio ir hierarchinio reikšmingumo, ribų ir klasterių sudėties stabilumo fiksuoto jautrumo analizės rezultatuose bei suderinamumo su kitomis JAV mioceno žinduolių biogeografinėmis schemomis (pvz. (Alroy, 1998; Shotwell, 1961; Tedford et al., 2004) ir jų ribų suderinamumo su žinomais mioceno geografiniais barjerais (Uolinių Kalnų grandinė, Apalačių kalnai, jūrinio klimato ribos, Baseinų ir kalnagūbrių provincija, Rio Grandė rifto sritis bei vulkaniškai aktyvios zonos JAV šiaurės vakaruose) interpretuoti kaip intrakontinentiniai mioceno žinduolių geobiomai.

Padalinimų silpnumas Centrinių Lygumų bioregione aiškintas geografinių barjerų trūkumu ir atitinkamai didesnėmis žinduolių faunos maišymosi erdvėje galimybėmis.

Išvados

Tyrimas atskleidė mioceno žinduolių JAV hierarchinę Bretskišką bioregionalizaciją ir tris pagrindinius jos bioregionus: Pietrytinę JAV, Vakarų Pakrantę ir Centrines Lygumas. Šie bioregionai interpretuoti kaip žinduolių intrakontinentiniai geobiomai – Bretskio hierarchijos vienetai. Taigi, šis tyrimas suteikė empirinį pagrindimą Bretskio hierarchijos teorijai ir įrodė, kad jos vienetai gali būti atpažįstami, kartografuojami ir analizuojami empirinių paleontologinių aptikimų taksonominių duomenų pagrindu taikant disertacijos metu sukurtus metodus. Atskleisti geobiomai gali būti naudojami kaip teritoriniai vienetai imčių sudarymui ateities tyrimuose.

3.3.2. Mulde/lundgreni įvykio trukmė ir struktūra

Antrasis HespDiv metodas *birese* buvo kritinis Mulde/*lundgreni* biotinio įvykio trukmės ir laikinės biotinės struktūros tyrime, atliktu sudarytos geochronologijos ir aukštos stratigrafinės raiškos ostrakodų taksonominio gausumo duomenų iš Gėluva-118 gręžinio pagrindu (Rinkevičiūtė et al., 2025). Tyrimo tikslas buvo šių duomenų pagrindu kiekybiškai atskleisti Mulde/*lundgreni* įvykio trukmę ir laikinę struktūrą. Anksčiau buvo atliktas tik pusiau kiekybinis šio įvykio trukmės įvertinimas (Cramer et al., 2012), o laikinė įvykio struktūra ostrakodų bendrijų pagrindu nebuvo žinoma.

Geologinė aplinka

Gėluva-118 gręžinys yra centrinėje-vakarų Lietuvoje (pav. 35), o tirtas gręžinio intervalas apima Rigos (Jaagarahu regioninis aukštas, vidurinis homeris) ir Gėluvos (Gėluvos regioninis aukštas, viršutinis homeris) svitas (pav. 34) (Rinkevičiūtė et al., 2022). Svitų litologinė sudėtis (mergelis su palaipsniui varijuojančia molio priemaiša) atspindi agradacinę šelfinę aplinką (Rinkevičiūtė et al., 2022). Vėlyvajame venloke ir ludlovyje, gręžinio vieta būtų lokalizuota sekliame šelfe palei pietvakarinį Baltikos paleokontinento pakraštį, rytinėje Silūro Baltijos Baseinos dalyje (pav. 35). Tuomet Baltikos kontinentas buvo žemose platumose (Torsvik & Cocks, 2013) ir pasižymėjo ekvatorinėmis sąlygomis, palankiomis turtingai kalcitinei bentosinei faunai.

Duomenys

Tyrimo duomenų pagrindą sudaro 44 aukštos stratigrafinės raiškos (20 cm) taksonominiai ostrakodų gausumo mėginiai, surinkti iš 1008 – 1018.8 m gylių intervalo, bei rečiau imti (kas 80 cm), seniau publikuoti (Rinkevičiūtė et al., 2022) 97 mėginiai, surinkti iš platesnio intervalo (952.1 – 1049 m). Duomenų rinkimą ir taksonominę analizę atliko S. Rinkevičiūtė. Detaliam ištyrimui 10.8 m intervalas buvo pasirinktas toks, kad maždaug per vidurį apimtų apytikslę anksčiau nustatytą Mulde/*lundgreni* įvykio gręžinyje vietą (Rinkevičiūtė et al., 2022). Gausumo taksonominius duomenis iš viso sudarė 31 rūšies 24587 individai.

Gręžinio geochronologija buvo sudaryta S. Radzevičiaus, naudojant įvairius chronostratigrafinius markerius ir sudarytą Gėluvos-118 gręžinio koreliaciją su Viduklė-61 ir Šiupyliai-69 gręžiniais. Geochronologiją sudaro: litostratigrafinė landoverio-venloko riba – 1120.5 m, Grötlingbo bentonito gylis suprojektuotas iš Viduklė-61 gręžinio, biostratigrafiškai nustatytas homerio padas – 1059 m, biostratigrafiškai nustatyta venloko-ludlovio riba – 930 m.

Metodai

Siekiant ostrakodų bendrijų kaitos pagrindu išskirti tikslų Mulde/*lundgreni* biotinio įvykio intervalą ir jo stadijas buvo pritaikytas *birese* metodas. Naudota palyginimo funkcija matavo Morisita-Horn panašumą, o reikalaujamas minimalus stebėjimų skaičius segmente buvo 10.

Siekiant išskirti ir biotiškai apibūdinti Mulde/*lundgreni* įvykio stadijas buvo paskaičiuotos šios biometrikos: suminis ostrakodų gausumas, rūšių turtingumas (angl. *species richness*), atvirkštinis Simpson‘o indeksas (1/D) bei Pielou tolygumas (angl. *Pielou evenness*).

Siekiant apibūdinti kiekvienos išskirtos Mulde/*lundgreni* įvykio stadijos ostrakodų paleobendrijas, 1000 kartų atsitiktinai iš stadijos intervalo buvo traukiami 3 atsitiktiniai stebėjimai ir išvedamas jų vidurkis kiekvienai biometrikai, t.y. pritaikytas taip vadinamas „bootstrap“ metodas. Šių vidurkių pasiskirstymai atvaizduoti Kartezinėse biometrikų plokštumose.

Siekiant apskaičiuoti Mulde/*lundgreni* biotinio įvykio atskirų stadijų trukmes ir bendrą įvykio trukmę bei trukmių didžiausio tikimybės tankio intervalus, pagal sudarytą Gėluvos-118 gręžinio geochronologiją, buvo sukurtas Bajesinis amžiaus-gylio modelis. Tam pasitelktas gilaus laiko analizėms pritaikytas ‘modifiedBChron’ R paketas (versija 0.7.0; Trayler et al., 2020). Mulde/lundgreni įvykio ir jo stadijų trukmės buvo išgautos iš aposteriorinio sedimentacijos laikų pasiskirstymo. Iš šių duomenų taip pat buvo paskaičiuotas laiko eilutės Naikvisto dažnis (angl. *Nyquist frequency*), siekiant sužinoti, kokios laikinės raiškos signalai dar gali būti iš jos patikimai išgaunami.

Rezultatai

Segmentavimo rezultatai su *birese* atskleidė, kad intervalas tarp 1016.3 m to 1009.1 m, pasižymi išskirtinai dideliais ostrakodų bendrijų pokyčiais (pav.

36). Tad šis intervalas buvo klasifikuotas kaip atspindintis Mulde/*lundgreni* įvykį.

Biometrikų pagrindu tarp 1015.1 ir 1012.3 m išskirtas Maksimalaus Streso Mulde/*lundgreni* įvykio stadija. Šiame intervale 8 mėginiai buvo be jokių individų, o likusiuose 4 intervalo mėginiuose buvo tik viena rūšis.

Šių dviejų intervalų pagrindu išskirta Kolapso stadija (1016.3 – 1015.1 m) ir Atsistatymo stadija (1012.3 – 1009.1 m).

Šių stadijų trukmių medianos ir jų 95% didžiausio tikimybės tankio intervalai (95% HDI) išgauti iš Bajesinio amžiaus-gylio modelio (pav. 37): Kolapso – 50 tūkst. m. (11-171 tūkst. m.), Maksimalaus Streso – 120 tūkst. m. (31-601 tūkst. m.), Atsistatymo – 80 tūkst. m. (21-576 tūkst. m.) ir viso įvykio – 260 tūkst. m. (100-1136 tūkst. m.). Duomenų eilutės Naikvisto dažnis (mediana – 13 tūkst. m., 95% HDI: 2.5-75 tūkst. m.) buvo pakankamas (žr. išplėstinę argumentaciją papildomoje Rinkevičiūtė et al. (2025) medžiagoje).

Mulde/*lundgreni* įvykio stadijų ir įvykį supančių gręžinio intervalų ostrakodų paleobendrijos pasižymėjo skirtingais biometrikų pasiskirstymais Kartezinėse biometrikų plokštumose (pav. 38). Maksimalaus Streso stadijos biometrikos indikavo ryškų bendrijų kolapsą (nulinės Pielou tolygumo ir atvirkštinio Simpson‘o vertės, labai mažas, diskretizuotas gausumo pasiskirstymas). Kolapso stadijos bendrijų biometrikos buvo panašios į bendrijų, iš intervalo prieš Mulde/*lundgreni* įvykį, biometrikas, o Atsistatymo stadijos bendrijų biometrikos buvo panašios į bendrijų, iš intervalo po įvykio, biometrikas, tačiau Mulde/*lundgreni* įvykio stadijose Pielou tolygumas buvo išaugęs, o gausumas nukritęs lyginant su gretimais įvykiui intervalais. Ostrakodų bendrijos prieš Mulde/*lundgreni* įvykį pasižymėjo kiek mažesniu gausumu, mažesniu atvirkštiniu Simpson‘o indeksu ir ženkliai mažesniu Pielou tolygumu nei bendrijos po įvykio.

Diskusija

Nustatyta tikėtina Mulde/*lundgreni* įvykio trukmė yra maždaug keturis kartus trumpesnė nei ankstesni pusiau kiekybiniai skaičiavimai pagal (Cramer et al., 2012), kur gauta trukmė siekė 1 mln. m.

Gauti rezultatai svarbūs ir tuo, kad įvykis mažai tyrinėtas pagal bentosinės faunos duomenis (Calner et al., 2012), o ankstesni tyrimai, greičiausiai dėl pernelyg prastos stratigrafinės raiškos ir paties įvykio trumpumo, rodė, kad įvykis neturėjo reikšmingo poveikio bentosinei faunai (Jeppsson et al., 1995). Šio tyrimo rezultatai atskleidė, kad ostrakodų paleobendrijos įvykio metu patyrė didelių pokyčių per itin trumpą laiką.

Atskleista ostrakodų bendrijų dinamika (pav. 38) gerai dera su koordinuotos stazės hipoteze, kuri numato ilgus jūrinių bendrijų stabilumo laikotarpius, pertrauktus staigių makroevoliucinių restruktūrizacijos įvykių (Brett, 2012). Interpretuota, kad du faktoriai buvo atsakingi už nustatytas tendencijas biometrikų kaitoje: „pusiausvyros trauka“ ir „ekologinis stresas“. Maksimalaus Streso stadijos metu ostrakodų bendrijos buvo lokaliai išnaikintos ir jos metu patyrė esminę makroekologinę restruktūrizaciją – ši stadija skiria ostrakodų paleobendrijas, apibūdinamas skirtingomis pusiausvyros būsenomis. Interpretuota, kad šiomis skirtingomis pusiausvyros būsenomis apibūdinamos ostrakodų bendrijos iš Mulde/*lundgreni* įvykio intervalo papildomai buvo paveiktos ekologinio streso, kuris ir lėmė mažesnį jų gausumą ir didesnį Pielou tolygumą.

Segmentavimo rezultatas (pav. 36) gali būti interpretuotas kaip laikinis pjūvis per erdvėlaikinę Bretskio hierarchiją. Maksimalaus Streso stadija šioje interpretacijoje atitinka ribą tarp dviejų stambaus masto ostrakodų geobiomų: „Senos pusiausvyros bendrijos + Kolapso stadijos bendrijos“ ir „Atsistatymo stadijos bendrijos + Naujos pusiausvyros bendrijos“. Savo ruožtu šie aukštesnio rango geobiomai sudaryti iš geografiškai mažų, nestabilių ir trumpai egzistavusių Mulde/*lundgreni* įvykio stadijų geobiomų (Kolapso ir Atsistatymo) bei geografiškai didelių, stabilių ir ilgai egzistavusių geobiomų, nepaveiktų Mulde/*lundgreni* įvykio. Šių geobiomų trukmę leidžia numatyti turimas amžiaus-gylio modelis, o geografinį dydį – Bretskio hierarchijos teorijos numatomas teigiamas ryšys tarp geobiomų dydžių ir jų trukmės (Spiridonov & Eldredge, 2024). Taigi, tyrimo rezultatai atskleidžia tikėtiną geobiomų hierarchijos dinamikos modelį tokių trumpų, bet reikšmingų biotinių įvykių metu kaip Mulde/*lundgreni* įvykis: ilgai egzistavę ir dideli geobiomai šių įvykių metu fragmentuojasi į dinamiškus, nestabilius ir mažus geobiomus, kurie pasibaigus perturbacijai vėl suauga į stabilius, didelius ir ilgalaikius geobiomus.

Išvados

Sukurta ir tyrime pritaikyta *birese* metodika suvaidino reikšmingą vaidmenį. Ji leido identifikuoti Mulde/*lundgreni* įvykio intervalą Gėluva-118 gręžinyje, bei šio įvykio stadijas. Tai buvo pagrindas skaičiuojant biotinio įvykio trukmę ir charakterizuojant įvykio laikinę struktūrą pagal ostrakodų taksonominius gausumo duomenis. Taip pat gautas hierarchinis ostrakodų laiko eilutės segmentacijos rezultatas atskleidė hipotetinį geobiomų hierarchijos dinamikos modelį trumpų ir reikšmingų biotinių įvykių metu.

Kiekybiškai paskaičiuota tikėtina Mulde/*lundgreni* įvykio trukmė (260 tūkst. m.) kelis kartus trumpesnė nei ankstesnis pusiau kiekybinis vertinimas (~ 1 mln. m.) (Cramer et al., 2012).

Taip pat nustatyta, kad įvykio metu ostrakodų bendrijos patyrė itin reikšmingų pokyčių. Tokio masto pokyčių visai nestebėta kituose tirtuose gręžinio intervaluose.

3.4. HespDiv Metodų Vertinimas

Disertacijoje HespDiv metodai įvertinti teoriniu, metodologiniu ir praktiniu požiūriu. Pirmiausia parodyta, kad jie atitinka Bretskio hierarchijos teorijos principus – generuoja hierarchinius, erdvėje ar laike vientisus vienetus, išvestyje pateikia ribas. Taip pat jie leidžia lanksčiai apsibrėžti padalinimo metodą ir priima didelę įvairovę duomenų tipų ir struktūrų. Tokiu būdu galima testuoti rezultatų tvirtumą (tikrinant rezultatų priklausomybę nuo padalinimo metodo ar duomenų transformacijos), tirti kitokio pobūdžio hierarchines sistemas (pvz., rūšių–aplinkos sąryšius, geocheminius ar sedimentologinius duomenis) ir netgi aptikti bei išspręsti Simpson‘o paradokso (Simpson, 1951) apraiškas laike ir erdvėje. Be kita ko, kitaip nei populiariausi bioregionalizacijos metodai jie nepriklauso nuo išankstinio aptikimo ar gausumo duomenų apdorojimo redukuojant juos į panašumų ar skirtumų matricą. Dėl šios priežasties HespDiv rezultatai dažnu atveju yra lengviau interpretuojami. Visos šios savybės išskiria HespDiv metodus nuo tradicinių bioregionalizacijos ir ribų aptikimo metodų (lentelė 2).

Paketas „hespdiv“ suteikia ir išskirtines rezultatų *post-hoc* analizių galimybes: ribų reikšmingumo ir jautrumo vertinimą, taksonų ar taksonominių grupių poveikio bioregionalizacijai vertinimą bei įvairias vizualizacijas. Gauti HespDiv poligonai gali būti panaudojami kaip teritoriniai vienetai ar įvestis kitose analizėse (pvz., istorinės biogeografijos DEC ar DIVA metoduose).

3.5. Ateities Perspektyvos ir Plėtojimas

HespDiv metodai turi didelį potencialą tolimesniam plėtojimui. Pagrindinės keturios vystymo kryptys – didesnis efektyvumas, našumas, patikimumas bei platesnės išvesties apdorojimo ir tolimesnių analizių galimybės. Iteracinė algoritmo struktūra su dinamiškai besiplečiančia įvestimi vietoje rekursinės algoritmo struktūros jau pasiteisino *birese* algoritme ir turėtų padidinti kodo stabilumą kituose HespDiv metoduose. Paraleliniai skaičiavimai (angl. *parallel processing*) turėtų kartais sumažinti skaičiavimo trukmę tiek pagrindiniuose skaičiavimuose, tiek jautrumo analizėse. Tokie skaičiavimai jau buvo integruoti naujausios paketo versijos *hespdiv* rezultatų jautrumo analizėse ir sėkmingai sumažino skaičiavimo trukmę ~10 kartų. *Birese* metodo duomenų skaidymo vienmatėje erdvėje logikos eksportavimas į dvimatę ar trimatę erdvę priveda prie Thiessen‘o poligonų taikymo skirstant duomenis į erdvėje ar erdvėlaikyje vientisus poabius. Taigi, erdvinių ir erdvėlaikinių ribų generavimo srityje perspektyvi yra Thiessen‘o poligonų ir Delaunay trianguliacijos taikymo kryptis, nors dabartinė *hespdiv* realizacija kai kuriais atvejais išlieka pranaši. Thiessen‘o poligonų pagrindu generuojamų padalinimų pranašumas būtų tas, kad tokie padalinimai apibrėžtų visus unikalius erdvėje ar erdvėlaikyje vientisus duomenų poaibius. Tokiu principu gauti padalinimai būtų patikimesni ir geometriškai bei topologiškai įvairesni, tačiau jų testavimas reikalautų papildomų optimizaciją pagreitinančių sprendimų.

Siekiant atskleisti HespDiv metodų perspektyvas ir juos toliau plėtoti taip pat būtini nauji atvejų tyrimai, apimantys ne tik skirtingus laikotarpius ar taksonomines organizmų grupes, bet ir abiotinius duomenis (pvz., geocheminius, sedimentologinius) bei taikymo sritis, kuriose tradiciniai metodai neveiksmingi (pvz. sprendžiant erdvines ar laikines Simpson‘o paradokso apraiškas).

Taigi, disertacija sudaro pagrindą ilgalaikei metodologinių ir taikomųjų tyrimų programai, kurios metu bus galima nuodugniau ištirti HespDiv šeimos metodų galimybes ir atskleisti naujas įžvalgas apie biotos bei kitų hierarchinių sistemų organizaciją.

Išvados

Šioje disertacijoje apjungiant teorinius ir metodologinius sprendimus gilinamasi į biotos organizacijos erdvėje ir laike prigimtį.

Apžvelgus disipacinių sistemų, energijos gradientų ir fizinių esinių daugiamastelinių, erdvėje lokalizuotų sąveikų principus, padaryta išvada, kad hierarchijų teorija yra tinkama ir efektyvi teorinė prieiga tiek biotinių, tiek abiotinių sistemų sandaros tyrimams. Bretskio hierarchija identifikuota kaip tinkamiausia teorija biotinių sistemų, stipriai integruotų su abiotine aplinka, tyrimams.

Šioje disertacijoje Bretskio hierarchijos vienetai buvo išskirti empiriškai naudojant sukurtą metodinę HespDiv prieigą. Jos metodai – *hespdiv*, *birese* bei papildomos jų rezultatų analizės funkcijos „hespdiv“ R pakete – leidžia atskleisti empirinę Bretskio hierarchiją (čia pavadintą Bretskiškąją hierarchija) bei jos pagrindu atskleisti ontologinės Bretskio hierarchijos vienetus ir jų hierarchinę organizaciją. Pritaikius sukurtus metodus kiekybiškai apibrėžti trys mioceno žinduolių geobiomai JAV (Vakarų pakrantės, Centrinių lygumų ir Pietryčių JAV) bei ostrakodų taksonominių gausumo duomenų pagrindu identifikuota šešių geobiomų hierarchinė laikinė organizacija, būdinga Baltijos Silūro Baseino rytinės dalies teritorijai.

Disertacijoje taip pat pristatyti metodai, galintys kiekybiškai įvertinti biogeografinių vienetų ribų blausumą. Atskleista, kad intrakontinentiniai mioceno žinduolių geobiomai JAV teritorijoje pasižymi blausiomis ribomis.

Birese metodo su Bajesiniu amžiaus–gylio modeliavimu integracija leido patikslinti Mulde/*lundgreni* biotinio įvykio trukmę (260 tūkst. m.) ir ostrakodų gausumo duomenų pagrindu charakterizuoti įvykio laikinę struktūrą. Taip pat šios metodinės integracijos rezultatų interpretacija privedė prie naujos hipotezės apie geobiomų dinamiką trumpų, bet reikšmingų ekologinių perturbacijų metu, t.y. stambūs, stabilūs ir ilgalaikiai geobiomai tokių krizių metu fragmentuojasi į trumpalaikius, mažus ir nestabilius geobiomus.

Sukurti metodai prieinami mokslo bendruomenei per atviro kodo R paketą „hespdiv“ bei viešai paskelbtą *birese* kodą, užtikrinantį platų taikymą, skaidrumą ir rezultatų atkuriamumą (angl. *reproducibility*).

Metodai sukurti taip, kad būtų lankstūs ir plataus pritaikomumo. Jie priima įvairios kilmės, tipo ir struktūros duomenis, o jų hierarchiniams skaidymams galima naudoti laisvai apibrėžiamą palyginimo funkciją. Toks dizainas ženkliai praplečia potencialią HespDiv metodų nišą už biogeografijos ribų.

Disertacija susieja Bretskio hierarchijos teoriją su empiriniais duomenimis, apžvelgdama kada, kaip ir kokiu patikimumu iš paleontologinių duomenų galima rekonstruoti geobiomus. Joje atskiriamos empirinės, diachroniškos (laike suvidurkintos) Bretskiškos bioregionų hierarchijos nuo ontologinės, anastomozinės Bretskio geobiomų hierarchijos. Atkreipiamas dėmesys į realų biotinių sistemų ir tuo pačiu Bretskio hierarchijos sudėtingumą, kuris gali lemti, kad kai kada stambūs geobiomai gali persidengti erdvėje.

Apibendrinant, disertacija transformuoja Bretskio hierarchijos teoriją iš konceptualaus modelio į empiriškai testuojamą ir taikomą paradigmą.

PADĖKA

Prieš pradėdamas visiems dėkoti, norėčiau atsiprašyti. Nemėgstu demonstruoti sentimentalumą, pažeidžiamumą ir jautrumą. Už tai retai, labai retai nuoširdžiai kam nors dėkoju už svarbius dalykus. Tad pirmiausia atsiprašau už tai. Kadangi šiuo klausimu taisytis neketinu bei nemėgstu kartotis, visiems šios padėkos adresatams greičiausiai teks pasitenkinti šia rašytine padėka. Už tai irgi atsiprašau – Jūs tikrai visi verti gyvai ištartos ir ne vieną kartą pakartotos nuoširdžios padėkos.

Jau bakalauro pirmaisiais metais norėjau išbandyti mokslinį darbą. Tik nežinojau nuo ko pradėti ir kaip. Tas noras taip ir būtų likęs svajone, jei ne Andrej Spiridonov. Jis pasiūlė įdomią, ambicingą ir iššūkiais prisotintą mokslinę problemą-bakalaurinio darbo temą bei tapo mano mokslinio darbo vadovu. Nuo to laiko taip ir tebesiūlo vis aukštesnio kalibro mokslines problemas-temas, skatina kelti sunkius klausimus ir toliau vadovauja atliekant tyrimus, vis išmokydamas arba suteikdamas galimybes išmokti arba atrasti naujų įdomių dalykų. Už tai esu be galo dėkingas ir dėkoju.

Esu dėkingas ir dėkoju savo šeimai, tėvams bei kitiems artimiesiems ir draugams už palaikymą, priežiūrą, ugdymą ir laiką kartu. Be šių dalykų ne tik, kad nebūtų šios disertacijos, bet nebūtų ir manęs labai tiesiogine prasme – Jūs mane užauginote ir nuolat lydėjote per gyvenimą. Tad tikiu, kad didele dalimi suformavote mano charakterį – tokį kurio reikėjo, kad pasukčiau mokslo keliu. Taigi, didelis ačiū Jums.

Taip pat esu dėkingas ir dėkoju savo esamiems bei buvusiems kolegoms ir dėstytojam: Laurui Balakauskui, Simonai Bekeraitei, Antanui Brazauskui, Giedriui Bičkauskui, Audriui Čečiui, Nikitai Dobrotin, Sonatai Gadeikienei, Rimantei Guobytei, Donatui Kaminskui, Arūnui Kleišmantui, Jurgai Lazauskienei, Gediminui Motuzai, Sigitui Radzevičiui, Simonai Rinkevičiūtei, Eugenijai Rudnickaitei, Giedrei Vaikutienei, Gražinai Skridlaitei, Robertui Stankevič, Petrui Šinkūnui. Kiekvienas man buvo kaip mentorius ir pavyzdžiais, pokalbiais, pa(si)tarimais bei pamokymais ir paskaitomis išmokino mane ne tik įvairių dalykinių žinių bei pakurstė smalsumą tomis kryptimis, bet ir paprastų buitinių-gyvenimiškų dalykų ir naudingų perspektyvų į darbą, mokslą, gyvenimą.

Išskirtinis ačiū recenzentams Antanui Brazauskui ir Donatui Kaminskui, kad skaitėte mano disertaciją, gilinotės į jos temą bei davėte konstruktyvių ir naudingų pastabų, kurios tikiu, kad padarė šią disertaciją geresnę ir pravers rašant bei planuojant kitus mokslinius darbus.

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EGU General Assembly 2024, Vienna, Austria (2024). **Poster presentation:** "Deciphering the dynamics of the Mulde Event—Bayesian ultra-high-resolution ostracod paleocommunity analysis"

Palaeoverse Hackathon, 7th–8th September 2023, University College London, London, United Kingdom (2023), **attendee.**

EGU General Assembly 2023, Vienna, Austria (2023). **Poster presentation**: “"HespDiv" method allows to quantify the dark matter of biosystems”
3rd Crossing Ecological - Palaeontological Gap 2023 symposium, Vilnius, Lithuania, (2023). **Oral presentation**: “THE “HESPDIV” R PACKAGE: CASE STUDY OF MIOCENE MAMMAL BIOGEOGRAPHY IN US”.
5th International meeting of early-stage researchers in palaeontology, Vilnius, Lithuania (2021). **Oral presentation:** “Report of ichnofossils found in the aeolian dunes and sand sheets of Lithuania”
Daumantas, L., and Spiridonov, A., Hierarchical spatial data subdivision methods family – «HespDiv» – is coming to garnish the toolkit of numerical palaeontologists, in Proceedings 65th Palaeontological association annual Meeting, the university of Manchester, 2021 December 18-20 2021, The Palaeontological Association. **Poster presentation.**
20th Congress of the International Union for Quaternary Research (INQUA). Dublin, Ireland (2019). **Poster presentation**: “Dynamics of prehistoric settlement regional patterns governed by cultural and environmental factors in the south east Baltic territory (Lithuania)”
Annual Conference of PhD Geology Students. Vilnius, Lithuania (2019). **Oral presentation:** “MAŠININIS REKURSYVUS PALEONTOLOGINIŲ DUOMENŲ ERDVINĖS ANALIZĖS ALGORITMAS”. Title in English: “A Machine Recursive Algorithm for the Spatial Analysis of Palaeontological Data”.
62nd International Conference for Students of Physics and Natural Sciences: OPEN READINGS 2019. Vilnius, Lithuania (2019). **Poster presentation:** “MACHINE LEARNING APPLICATIONS IN HUMAN LANDSCAPE PALAEOECOLOGY”
GIS Švietimui 2019. Vilnius, Lithuania (2019). **Oral presentation**: “Mašinio mokymo metodų taikymas priešistorinių gyvenviečių pasiskirstymo analizėse**”**. Title in English: “Application of Machine Learning Methods in the Analysis of Prehistoric Settlement Distribution”.
Annual Conference of PhD Geology Students. Vilnius, Lithuania (2017). **Oral presentation**: “Geologiniai ir geomorfologiniai priešistorinių žmonių gyvenviečių veiksniai”. Title in English: “Geological and Geomorphological Factors of Prehistoric Human Settlements”.
SCIENCE STARTUP. Vilnius, Lithuania (2017). **Oral presentation:** “Geologiniai ir geomorfologiniai veiksniai priešistorinių žmonių gyvenviečių pasiskirstymui”. Title in English: “Geological and Geomorphological Factors Influencing the Distribution of Prehistoric Human Settlements”.
Lithuanian Esri User Conference. Vilnius, Lithuania (2017) **- attendee**

GIS Švietimui 2017. Vilnius, Lithuania (2017). **Oral presentation**: “GIS panaudijmas tiriant geologinių ir geomorfologinių veiksnių įtaką priešistorinių žmonių pasiskirstymui po kraštovaizdį”. Title in English: “Applying GIS in studies of geological and geomorphological factors influence on prehistoric human distribution across the landscape”.

Membership in Professional Societies:

The Geological Society of Lithuania (Lithuania, Vilnius) (since 2013)

Grants and Prizes:

- Grant for research event: “3rd Crossing Palaeontology-Ecology Gap” symposium. Received from the “Go Vilnius” international conference funding program. **2023**. [4,000 €].
- Grant for research event: “3rd Crossing Palaeontology-Ecology Gap” symposium (S-MOR-23-12). Received from Lithuanian Research Council. **2023**. [10,395 €].
- Grant for research. **2018**. Development and application of classification and regression trees for the spatial studies of paleontological material. [~2,839 €]
- Award for the best presentation at SCIENCE STARTUP student conference (**2017**)

Membership in conference organizing committees:

- Hybrid Symposium on Approaches to Mass Extinctions (**2025**)
- 3rd Crossing the Palaeontological-Ecological Gap meeting (**2023**)
- 5th International Meeting of Early-stage Researchers in Palaeontology (**2021**)
- Nanostructured Bioceramic Materials (**2020**)
- Chemistry & Chemical technology. Lithuanian chemist conference (**2019**)
- Chemistry & Chemical technology. Nacional student conference (**2019**)

SCIENTIFIC PUBLICATIONS ON THE DISSERTATION TOPIC

Daumantas, L., and Spiridonov, A., 2024, hespdiv: an R package for spatially constrained, hierarchical and contiguous regionalization in palaeobiogeography: Palaeontology, v. 67, no. 3, p. e12702.

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Rinkevičiūtė, S., **Daumantas, L.,** Radzevičius, S., and Spiridonov, A., 2025, Bayesian analysis of ultra-high-resolution ostracod record reveals the tempo and structure of the late Wenlock Mulde Event: Lethaia, v. 58, no. 1, p. 1-11.

FOR NOTES

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