Biogeography, Ecological Theories in

F.M.C.B. Domingos[a], **D.C. Silva**[b], **and F.S. Caron**[a], [a] Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, PR, Brazil; and [b] Universidade do Estado de Mato Grosso, Nova Xavantina, MT, Brazil

This is an update of A.J. Rominger, Biogeography, Ecological Theories in, Editor(s): Richard M. Kliman, Encyclopedia of Evolutionary Biology, Academic Press, 2016, Pages 145–148, ISBN 9780128004265, https://doi.org/10.1016/B978-0-12-800049-6.00317-6.

Key Points

- This chapter aims at presenting the major scientific developments of theories in ecological biogeography, focusing on persistent ecological patterns observed in nature, and the causal relationship with the associated ecological and evolutionary processes.
- We introduce readers to island biogeography, the species-area relationship, geographic ranges and gradients of biodiversity, ecogeographic rules, and the theoretical ecological and evolutionary background that can explain these patterns.
- Biogeographic mechanisms behind community assembly processes in different spatial scales are discussed.
- Methodological advances and hypothesis testing of local and large-scale diversity patterns are presented.

Glossary

Adaptive radiation The process by which a single ancestral species rapidly diversifies into many new ecologically distinct species. Although many processes have been proposed to explain how it occurs, the consensus is that it should happen in a relatively short period of time and, obviously, through the action of natural selection.

Diversification From a macroevolutionary perspective, biological diversification refers to the large-scale evolutionary changes that occur over long periods of time, leading to the emergence of new species, genera, and higher taxonomic groups. Diversification is necessarily the consequence of many speciation events. The diversification rate of a group of organisms is usually understood as the speciation rate minus the extinction rate.

Ecological limits Constraints on the number of species that can coexist in a given environment due to factors such as resource availability, habitat space, and competition. These limits suggest that there is a maximum carrying capacity for species diversity within an ecosystem, beyond which additional species cannot be sustained.

Endemism The state of a species (or other taxonomic grouping, such as genera or subspecies) of being unique to a particular geographic location, such as an island, biome, or country, and not found naturally anywhere else in the world. The endemism status, thus, necessarily invokes a particular spatial scale on which the taxon is considered endemic.

Extinction The complete disappearance of a species from earth, such that no living individuals of that species remain. From a macroevolutionary perspective, the extinction rate refers to the number of taxa that go extinct during a certain period of time.

Fitness The ability of an individual to survive and reproduce in its natural environment, thereby passing on its genes to the next generation. It is often measured by the number of offspring an individual produces that survive to reproductive age.

Geographic range (of a species) The whole area or region where a particular species can be found. In biogeographic terms, this range includes all the locations where the species lives, breeds, and migrates.

Habitat The natural environment in which a particular species lives and thrives. It includes all the biotic (living) and abiotic (non-living) factors that affect the species, such as climate, soil, water, and other organisms.

Speciation The evolutionary process by which populations evolve to become distinct species. Speciation is necessarily a demographic process caused by the action of evolutionary mechanisms such as natural selection and genetic drift.

Species diversity A measure of the number and abundance of different species within a particular area or ecosystem. It encompasses both species richness (the number of species) and species evenness (the relative abundance of each species).

Species richness The number of different species present in a particular area or ecosystem. It is a straightforward measure of biodiversity and indicates the variety of life forms in a given place.

Stochastic Refers to processes that are randomly determined and involve a degree of unpredictability. In biological contexts, stochastic events can influence genetic variation, population dynamics, and evolutionary outcomes.

Key Points

Ecological biogeography research seeks to integrate ecological and evolutionary theories to understand the distribution and diversity of organisms on Earth. Some fundamental concepts in biogeography and ecology, such as the species-area relationship that posits species richness increases with area, reflect widespread biodiversity patterns observed in nature. Identifying the biological processes responsible for producing these patterns requires integrating theoretical and empirical research on ecology and evolutionary biology. In the case of biogeography, the patterns of interest concern repeatedly documented arrangements in the distribution of species and biodiversity across geographic space. The ecological theories in biogeography provide the scientific background for researchers to estimate how organisms' interactions with their environment and each other shape biodiversity patterns across different spatial and temporal scales.

Introduction

If you ever study the distribution of biological diversity on Earth, you will perceive some striking patterns. For example, tropical forests are usually regarded as home to a multitude of colorful and exquisite animals, but primarily for the fact that they hold most of the plant and animal species in the world. In the endeavour of researching such intriguing patterns, you might ask "why are there so many species in the tropics"? Or maybe the right question is "why are there more species in the tropics compared to temperate regions"? If you could travel in a straight line from the tropical region to the north pole (the trip could start either in Eurasia, Africa, or the Americas), a clear change in biodiversity would be found across the landscape. Interestingly, incredible biodiversity differences would also be observed if you were able to climb a very high mountain range, such as the Andes, starting from the lowland Amazon. Hence, more generally, you could also ask "why are there more species in some parts of the planet than in other parts"? In turn, this question raises another: how do we separate the world into "parts"? Consider islands, which are easily distinguishable "parts" of the world, as their limits are clearly defined by the water that surrounds them. If you could travel between the many islands of the Indo-Australian Archipelago, from Borneo to Sulawesi, you would be able to observe wonderful differences in the animal species between these places. However, such distinct patterns are not as pronounced in most geographic circumstances. Drawing a line between different "parts" of the world is often complex because boundaries can be determined by multiple criteria, and may change depending on the spatial scale under consideration. With that in mind, the questions you might ask come to be continuously more complex: what determines biodiversity differences among different landmasses or continents? Why does biodiversity vary between latitudes, such as between tropical and temperate regions? Or even between different biomes, or between forests and savannas? In the Amazon region, for instance, you could literally walk from a savanna, with its particular animals, to the spectacular rainforest, which also holds its own unique set of animals. Well, the definition of forests and savannas is based on the differences between the organisms they hold, in this case, the proportion of trees and shrubs. Why do these distinct types of plants occupy different parts of the landscape? Is it due to the climate, or maybe to changes in the characteristics of the soil?

To answer the above questions, knowledge of tectonics, geology, climate, and especially the distribution of organisms is essential. This is exactly the subject of study in biogeography. As the discipline that investigates the distribution of organisms in space and time, biogeography is inherently at the intersection of ecology and evolutionary biology. One important aspect of biogeography research is that all questions must be answered considering specific spatial or geographic scales - patterns and processes acting in one scale might not hold in a different scale. We can observe changes in species number and composition on a very small geographic scale, for example between adjacent forest and savanna habitats in the tropical region (Freire-Jr et al., 2024), or over larger continental (Silva et al., 2024), and global scales (Falaschi et al., 2023). Biogeography is the science that explains how these patterns came to be, and how they are maintained over geological timescales. It uses the theoretical background of ecology and evolutionary biology to develop generalizations of biodiversity patterns and identify the core set of processes responsible for generating the patterns observed regarding the distribution of organisms and their traits.

Ecological Theories on Species Richness and Composition

A primary objective of ecology and biogeography is to investigate the patterns and drivers of species richness and composition across geographical regions and at different spatial scales. These patterns are influenced by geophysical characteristics, biological interactions, and historical processes, each operating at local, regional, and global scales. Prominent theories addressing these phenomena include the species-area relationship (SAR), the effects of speciation, the effects of island size and isolation on the distribution of organisms, and the latitudinal diversity gradient (**Fig. 1**).

Island Biogeography: Ecological and Evolutionary Dynamics

Island biogeography examines the ecological and evolutionary processes shaping species richness and composition in insular environments. MacArthur and Wilson's (1967) equilibrium theory of island biogeography proposes that species richness results from a dynamic balance between immigration and extinction rates, governed by island size and isolation. Larger islands support more species due to lower extinction rates and increased habitat diversity, while more isolated islands experience reduced immigration (**Fig. 1**). Over time, the theory was expanded to incorporate speciation as a critical driver of island biodiversity. On highly isolated islands with limited gene flow from the mainland, speciation often becomes the primary diversification mechanism, leading to endemic species and distinctive adaptive radiation (Whittaker et al., 2017).

More recent developments emphasize the dynamic nature of islands, where geological and climatic processes induce changes in size, elevation, and isolation. The General Dynamic Model (GDM) of oceanic island biogeography integrates these temporal dynamics, illustrating how phases of island emergence, development, and eventual subsidence shape patterns of species richness and endemism (Whittaker et al., 2017). This model predicts peak species diversity on islands of intermediate age, where habitat complexity is highest, and ecological opportunities are more abundant. Furthermore, archipelagos exhibit steep species-area relationships (SAR, see below), particularly for endemic taxa, driven by the combined effects of limited dispersal and localized speciation (Matthews et al., 2016). These advancements underscore the necessity of integrating ecological, evolutionary, and geological processes to unravel the complexity of island biodiversity.

Species-Area Relationship and Richness Dynamics

The species-area relationship (SAR) is one of the most well-established patterns in biogeography and ecology, positing that species richness should increase with the increase in the considered area. This pattern reflects underlying ecological and evolutionary processes acting across different spatial scales (Rosenzweig, 1995). Larger areas typically contain more species due to three primary mechanisms: the greater diversity of habitats in larger areas, which provides a broader range of ecological opportunities (Preston,

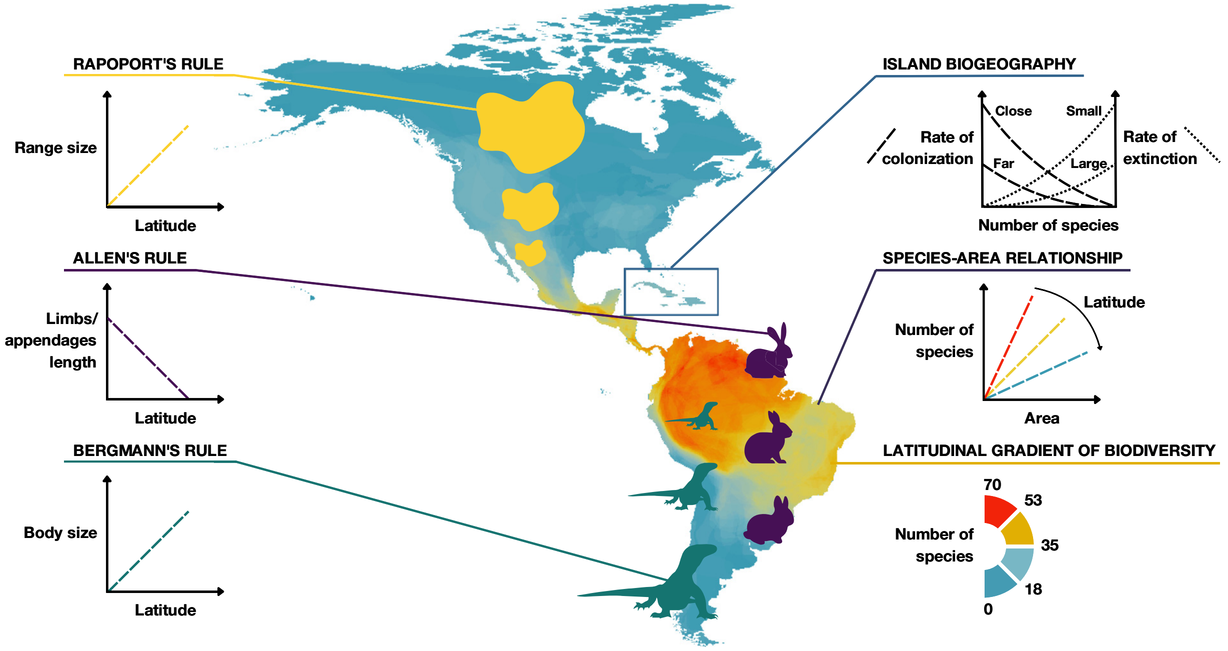

Fig. 1 Biogeographic and ecological patterns across the Americas. The map illustrates key ecogeographic rules and gradients: (1) Rapoport's Rule (top-left) showing a positive relationship between range size and latitude; (2) Allen's Rule (middle-left) depicting a negative relationship between limb/appendage length and latitude; (3) Bergmann's Rule (bottom-left) showing a positive relationship between body size and latitude. The Island Biogeography model (top-right) highlights the relationship between species richness, island size, and distance from the mainland. The Species-Area Relationship (middle-right) demonstrates how species richness increases with area, and how this relationship can vary across latitudes. The Latitudinal Gradient of Biodiversity (bottom-right) shows species richness peaking in the tropics (warmer colors), as illustrated in the heatmap that covers the American continent and the corresponding pie chart. Representative animal silhouettes illustrate morphological trends across latitudes according to Allen's (rabbits) and Bergmann's rules (lizards).

1962); reduced extinction rates, as populations in larger areas are less vulnerable to stochastic events; and the stabilizing effects of immigration, facilitating the establishment and persistence of newly arrived species (MacArthur and Wilson, 1967). Beyond these factors, speciation significantly influences the SAR by increasing species richness independently of the source pool of potential colonizers (Losos, 2009). In larger areas, population isolation and genetic divergence may promote speciation events, leading to a steeper accumulation of species with the increasing area (Losos and Schluter, 2000). The SAR and its determinants vary depending on the spatial scale under consideration. At local scales, it usually reflects ecological interactions such as competition and dispersal. At regional scales, processes like colonization and connectivity among communities become more prominent drivers. On a global scale, evolutionary dynamics, including speciation and extinction, play a dominant role in shaping the SAR (Rosenzweig, 1995).

Geographic Range and Latitudinal Gradient in Biodiversity Patterns

Patterns of species richness are closely linked to the latitudinal diversity gradient, one of the most consistent and well-documented phenomena in biogeography, where species richness is higher in the tropics and declines towards the poles. Several hypotheses have been proposed to explain this pattern (Pianka, 1966). Greater climatic stability in the tropics is thought to promote long-term diversification and persistence of species, while intense biotic interactions, such as competition and mutualism, drive specialization and enable the coexistence of several species within smaller areas (Janzen, 1967).

The size and structure of species' geographic ranges also play an important role in shaping biodiversity at different spatial scales. In the tropics, smaller geographic ranges are associated with higher species richness and a faster rate of species accumulation within limited areas (Stevens, 1989). This dynamic is particularly evident in patterns like the SAR, where smaller ranges lead to steeper SAR curves (**Fig. 1**), especially in tropical regions (Whittaker et al., 2007). Consequently, tropical regions exhibit not only higher overall diversity but also higher species turnover compared to temperate regions, highlighting the interplay of ecological and evolutionary processes in shaping biodiversity. The latitudinal diversity gradient, therefore, reflects contrasts in historical and ecological processes between tropical and temperate zones and the strategies by which species utilize the available space. This contributes to the complexity of biodiversity patterns observed across different spatial scales, emphasizing the importance of regional dynamics and large-scale evolutionary trends in structuring global biodiversity.

Ecogeographic Rules

From cautious examinations of species distribution throughout space, researchers have often unraveled ecological and biogeographical patterns of species occurrence and their traits. These patterns are commonly referred to as "ecogeographic rules", indicating their global occurrence and persistence across different taxonomic groups. Some of these ecogeographic rules have historically received more attention than others and have been tested more thoroughly, such as Bergmann's rule, Rapoport's rule, and Allen's rule. Interestingly, most of these patterns describe latitudinal variation of species traits, where latitude is usually a proxy for climate differences among regions. Bergmann's was one of the first biogeographic rules to be proposed (Bergmann, 1847). It posits a latitudinal gradient of body sizes, where large-bodied animals will occur in higher latitudes, whereas species with smaller body sizes will occur more frequently in low-latitude environments (**Fig. 1**). This increase in body size is also noted when analyzing species at increasing altitudes. The explanation for this pattern is usually based on the global temperature gradient, where in higher latitudes (and altitudes) species would evolve toward larger sizes because of the lower surface area to volume ratio, helping them to radiate less heat. Hence, Bergamnn's rule usually applies to endotherms (i.e., birds and mammals). Nonetheless, there is evidence for this rule on ectotherms, although they may frequently be contradictory, and the specific patterns much more complex. As a result, Bergmann's rule can be considered a species-dependent rule because it varies depending on the taxonomic group and geographic location.

Subsequently, Allen also studied how heat can affect endotherms' bodies by examining how their appendages may vary in size and form throughout the globe. Allen's rule posits that species' appendages should decrease in size as the species approaches the poles (Allen, 1877) (**Fig. 1**), also illustrating how the latitudinal gradient affects species traits due to climatic differences. The appendages would increase in size as the latitude decreases to improve heat dissipation in warmer regions. Again, this pattern is mostly based on birds and mammals, so any generalization to ectotherm taxa must be interpreted with caution. Another example of an ecogeographic pattern observed for terrestrial organisms is Rapoport's rule, positing that species tend to have larger range sizes as they approach higher latitudes or altitudes (Stevens, 1989) (**Fig. 1**). The reasoning behind the patterns is that regions with greater climatic variability, such as high latitudes and altitudes, enable species to evolve broader environmental tolerances, allowing them to inhabit larger areas. Contrary to the former two patterns, evidence for Rapoport's rule has been observed across multiple taxa, including plants, ectotherms, and endotherms, but not without several exceptions, reflecting the complexity of species distributions and their associated traits in natural environments.

Although latitudinal gradients are a major theme concerning ecogeographic rules, islands are also a pervasive study subject. The island rule, first proposed by Foster (1964) and later modified by Heaney (1978) and Lomolino (1985), states a tendency for dwarfism in species with large body sizes and gigantism in species with small body sizes when these species, originally from the mainland, colonize and evolve in insular environments. Different processes have been proposed to explain this pattern, including the lower predation pressure, relaxed competition, and a more severe limitation of resources on islands. However, although this rule has been historically advocated by many researchers, more recent and statistically congruent studies did not find evidence for the island rule in vertebrates or invertebrates, with only a few exceptions (Meiri et al., 2011). It has been shown that the largest species within lizard families and bird genera are insular, and a tendency for insular dwarfing in large mammals mainly at the genus level (Meiri et al., 2011). Hence, the common belief that islands have an unusually high number of size extremes might arise from the fact that gigantism and dwarfism are more noticeable when they occur on islands.

Lastly, we still lack an example of an ecogeographic rule that involves marine organisms. Marine organisms are also subjected to the effects of climate throughout the latitudinal gradient. One example is Thorson's rule (Thorson, 1936), which states the relationship between reproduction in benthic invertebrates and latitude. According to this rule, animals in lower latitudes should produce more eggs, developing pelagic and widely dispersing larvae. Contrastingly, higher latitude animals should produce few eggs and larger offspring, usually through viviparity. Even though this pattern was first observed and tested in marine invertebrates, it has also been demonstrated in marine vertebrates and terrestrial insects, such as butterflies.

It is hard to miss the fact that the rules described here are not general in the literal sense. In other words, there are many cases in which these rules do not hold, probably more than they do. This is not a way to propose that the terminology (i.e., "ecogeographic rules") should be abandoned. More importantly, it serves as a reminder that rules in ecology are (possibly always) contingent on some external factor (Lawton, 1999). This factor may be the taxonomic group, the geographic scale of the study, and/or other biotic or abiotic conditions of the environment. It is also important to notice that these patterns do not necessarily imply a process (Lawton, 1999). It is actually rather common that more than one ecological and evolutionary process is responsible for giving rise to the pattern in question. Possibly, the most pervasive patterns are the ones that have indeed more than one mechanism generating them. In essence, these ecogeographic rules are regularities seen in nature and their observation (or lack of) may be useful to describe the observable biodiversity patterns.

Processes Determining Species Richness and Composition in Ecological Communities

The relationship between species and their environment has long been addressed in studies of species ecological niches. The concept of the niche itself is one of the most debated ecological topics, with its definition continuously being modified over time. Grinnell is said to be the one who first described what a species' niche might be, defining it as the local variables that affect the presence of a species in a location (Grinnell, 1917). Subsequently, Elton presented another point of view on the niche, namely the trophic position of a species in a community (Elton, 1927). Hutchinson later advanced this discussion by proposing a central niche concept. In his definition, the niche is an abstract n-dimensional space where each axis represents an environmental variable within which a species can survive and thrive (Hutchinson, 1957). That is not to say the Hutchinsonian definition of the niche is correct. As of today, several other definitions of the niche have been established (e.g., Chase and Leibold, 2003; Soberon and Peterson, 2005; Whittaker et al., 1973). All these definitions share the assumption that the species composition of a particular community is determined by the ecological niches of such species.

Based on these foundational definitions, niche theory provides a framework for understanding how ecological niches influence community assembly processes. Niche theory can help explain why certain species exist in a community while others do not. Is it random, or is there some determinism involved? According to this theory, for species to coexist in a given community, they must present stabilizing niche differences facilitating their mutual persistence and relative fitness differences promoting competitive exclusion (HilleRisLambers et al., 2012). Differences in species' niches determine to which degree they can coexist in a community through resource partitioning, for instance. However, the specific niches of these species influence their differential fitness in a given context, which ultimately determines the outcome of their competition. In summary, niche theory explains community composition solely through the concept of species' niches.

Although the niche theory is a well-established framework for explaining species richness in a community, it is not the only one. Hubbell's neutral theory (Hubbell, 2001) posits that competition is not a significant force shaping community composition. In this context, the dynamics of a community are determined by drift, dispersal, and speciation. Interestingly, Hubbell developed this theory as an extension of MacArthur and Wilson (1967) theory of island biogeography, incorporating speciation into it. It is important to note that the specific composition of a community is neutral in this perspective. This is to say that if the "tape of life" were replayed, the resulting subset of species would likely differ. In this theory, variations among species in a community would arise due to differences in their abundances. Although Hubbell's theory helps provide a framework to test community assembly hypotheses, it assumes that species share identical fitness, niches, and selective pressures, which might not be supported by empirical evidence.

In reality, it is possible that neither a completely random nor deterministic explanation accurately describes the real determinants of community composition. Community composition may result from the interplay between niche and neutral processes. Undoubtedly, the biogeographic scale from which this process is studied will lend more support to one process than the other. In this context, local patterns may be more influenced by niche processes, while regional scales are likely determined by neutral factors. Thus, understanding community composition requires disentangling the contributions of niche and neutral processes while recognizing their interplay across scales.

The Potential Influence of Ecological Limits and Competition on Species Richness and Community Assembly

One of the most intriguing biogeographic phenomena is the vast variation of species richness among different geographic locations and spatial scales. This variation is determined by both present-day ecological (biotic and abiotic) interactions and the evolutionary history of the involved organisms. Only three mechanisms explain the presence of a particular species at any biogeographic scale:

speciation, extinction, and migration. Nonetheless, several ecological mechanisms can explain species diversity in a determined location at a given spatial scale, because their effect will influence species maintenance throughout time. As explained above, we currently have a good understanding of the ecological mechanisms that influence species richness at local and continental scales. However, there is one question that still attracts great debate: are biological communities bounded by any type of ecological limits? If so, there should be diversity-dependent mechanisms that regulate species richness, and these should be constrained by the total resource availability. As a result, biological communities are in a dynamic equilibrium throughout time. On the other hand, there is the argument that diversity is not in equilibrium, and rather unbounded by resource availability. In this case, biological communities should be unsaturated (open to new species) and constantly changing over time. While there is a strong and consistent theoretical background and mathematical models to support the first view (Rabosky and Hurlbert, 2015), there is still a lack of clear empirical evidence supporting the unbounded hypothesis (Harmon and Harrison, 2015).

Ecological biogeography is also interested in understanding how species' interactions with their environment and with other species might affect diversity at different geographic and temporal scales. In particular, another matter of dispute is the relevance of competition in determining species richness. Species competition is intuitively put forward as a mechanism influencing species maintenance and, hence, community assembly at local and regional scales. Many of these considerations were often advanced in a speculative fashion in the specialized literature, and empirical evidence on competition at the local scale is still scarce (Dayan and Simberloff, 2005). Models of species coexistence usually demand that resources are somewhat limited and that species interact in a way that competition for these resources is demographically detrimental (Chesson, 2000). In other words, competition could negatively influence individual fitness, in turn leading to reduced population size and, potentially, to local species extirpation. If these conditions are met, competition may also affect species richness from a macroevolutionary perspective, even though its effects are not direct, because competition will be acting on a different hierarchical level. For competition to regulate species richness over time on a macroevolutionary scale, diversification (speciation *minus* extinction) must be bounded by a theoretical maximum species diversity (Rabosky, 2013). In sum, although ecological theory is often based on assumptions that competition can play an important role in determining species richness and abundance, strong empirical evidence is lacking for most naturally occurring communities.

Hypothesis Testing in Ecological Biogeography

Biogeographers have long been interested not only in the number and distribution of species on Earth, but also in the organisms' associated traits and their variation (see Ecogeographic rules above). The use of species evolutionary relationships and the phylogenetic distribution of their associated functional traits provided invaluable evidence to unveil the ecological and evolutionary processes that determine the observed biodiversity patterns. Being so, the field of ecological biogeography has benefited from a plethora of methodological advances, facilitated by the development of modern statistical methods and software availability that provided the means to robustly test both old and novel biogeographic hypotheses. In particular, the growing accessibility to phylogenetic hypotheses generated using molecular data, as well as the museum or field-based collection and large-scale compilation of functional traits largely helped in the development of new research avenues. There are at least two biogeographic scales on which phylogenetic and functional information have been particularly useful for hypotheses-testing in the last few decades: (1) testing large-scale biogeographic patterns and ecogeographic rules (**Fig. 1**); and (2) testing community assembly hypotheses using information on the evolutionary relationships and functional traits of species in regional and local communities (Ruffley et al., 2019). Advances have been made, for example, by including phylogenetic information to test the latitudinal gradient of biodiversity (Wiens and Donoghue, 2004), and testing multiple phenotypic and physiological optima under an informed phylogenetic perspective in order to explain Bergmann's and Allen's rule (Rubalcaba et al., 2022).

While species richness (or taxonomic diversity), provides the most basic and important information biogeographers need to unveil biodiversity patterns, the advent of methods to estimate functional and phylogenetic diversity has facilitated important empirical advances to test ecological theories in biogeography. Functional diversity measures the degree of trait variability among species in a community and provides estimates of the relationship between the organisms' features and how they operate in the local ecosystem. Phylogenetic diversity measures the accumulation of evolutionary distinctiveness in a group of species and can be used to estimate the degree of evolutionary relatedness of the species on local and regional scales. Testing classic community assembly processes, namely biotic interactions and abiotic filtering (or the lack thereof; the neutral model), can be enhanced by using functional and phylogenetic diversity metrics. These metrics can improve the statistical resolution to identify the processes determining regional and local community composition. Functional diversity provides insights into how organisms respond to their abiotic environment, while phylogenetic diversity reveals the extent to which evolutionary history has shaped species composition. Together, these types of information offer evidence of the potential interactions and competition among species in a community by taking into account the evolution of similar adaptive traits.

Conclusion

Understanding species richness and abundance requires integrating ecological and evolutionary theories. The mechanisms that determine island biogeography patterns, species-area relationships, and latitudinal diversity gradients highlight the complex interplay of current ecological dynamics and historical evolutionary processes. The ecogeographic rules further illustrate how species traits and distributions are influenced by environmental gradients and diversification processes. While the integration of phylogenetic and functional diversity metrics has significantly advanced our understanding of ecological and evolutionary processes shaping biodiversity, this area is in constant methodological development and remains a fruitful area for future theoretical development.

References

Allen, J.A., 1877. The influence of physical conditions on the genesis of species. Radic. Rev. 1, 108—140.

Bergmann, K.G.L.C., 1847. Über die Verhältnisse der wärmeökönomie der Thiere zu ihrer Grösse. Gött. Stud. 3, 595—708.

Chase, J.M., Leibold, M.A., 2003. Ecological Niches: Linking Classical and Contemporary Approaches. University of Chicago Press, Chicago, IL.

Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. 31, 343—366. https://doi.org/10.1146/annurev.ecolsys.31.1.343.

Dayan, T., Simberloff, D., 2005. Ecological and community-wide character displacement: the next generation. Ecol. Lett. 8, 875—894. https://doi.org/10.1111/j.1461-0248.2005.00791.x.

Elton, C.S., 1927. Animal Ecology. Macmillan Co, New York, NY. https://doi.org/10.5962/bhl.title.7435.

Falaschi, M., Marta, S., Lo Parrino, E., Roll, U., Meiri, S., Ficetola, G.F., 2023. Global bioregions of reptiles confirm the consistency of bioregionalization processes across vertebrate clades. Glob. Ecol. Biogeogr. https://doi.org/10.1111/geb.13694 geb.13694.

Foster, J.B., 1964. Evolution of mammals on islands. Nature 202, 234—235. https://doi.org/10.1038/202234a0.

Freire-Jr, G. de B., Diniz, I.R., Salcido, D.M., Oliveira, H.F.M., Sudta, C., Silva, T., Rodrigues, H., Dias, J.P., Dyer, L.A., Domingos, F.M.C.B., 2024. Habitat heterogeneity shapes multiple diversity dimensions of fruit-feeding butterflies in an environmental gradient in the Brazilian Cerrado. For. Ecol. Manag. 558, 121747. https://doi.org/10.1016/j.foreco.2024.121747.

Grinnell, J., 1917. The niche-relationships of the California thrasher. The Auk 34, 427—433. https://doi.org/10.2307/4072271.

Harmon, L.J., Harrison, S., 2015. Species diversity is dynamic and unbounded at local and continental scales. Am. Nat. 185, 584—593. https://doi.org/10.1086/680859.

Heaney, L.R., 1978. Island area and body size of insular mammals: evidence from the tri-colored squirrel (callosciurus prevosti) of Southeast Asia. Evolution 32, 29. https://doi.org/10.2307/2407408.

HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M., Mayfield, M.M., 2012. Rethinking community assembly through the lens of coexistence theory. Annu. Rev. Ecol. Evol. Syst. 43, 227—248. https://doi.org/10.1146/annurev-ecolsys-110411-160411.

Hubbell, S.P., 2001. The unified neutral theory of biodiversity and biogeography. In: Monographs in Population Biology. Princeton University Press, Princeton.

Hutchinson, G.E., 1957. Concluding remarks. Cold Spring Harb. Symp. Quant. Biol. 22, 415—427. https://doi.org/10.1101/SQB.1957.022.01.039.

Janzen, D.H., 1967. Why Mountain passes are higher in the tropics. Am. Nat. 101, 233—249.

Lawton, J.H., 1999. Are there general laws in ecology? Oikos 84, 177—192.

Lomolino, M.V., 1985. Body size of mammals on islands: the island rule reexamined. Am. Nat. 125, 310—316. https://doi.org/10.1086/284343.

Losos, J.B., 2009. Ecology and adaptive radiation. In: Losos, J. (Ed.), Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles. University of California Press. https://doi.org/10.1525/california/9780520255913.003.0011, p. 0.

Losos, J.B., Schluter, D., 2000. Analysis of an evolutionary species—area relationship. Nature 408, 847—850. https://doi.org/10.1038/35048558.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press.

Matthews, T.J., Guilhaumon, F., Triantis, K.A., Borregaard, M.K., Whittaker, R.J., 2016. On the form of species—area relationships in habitat islands and true islands. Glob. Ecol. Biogeogr. 25, 847—858. https://doi.org/10.1111/geb.12269.

Meiri, S., Raia, P., Phillimore, A.B., 2011. Slaying dragons: limited evidence for unusual body size evolution on islands. J. Biogeogr. 38, 89—100. https://doi.org/10.1111/j.1365-2699.2010.02390.x.

Pianka, E.R., 1966. Latitudinal gradients in species diversity: a review of concepts. Am. Nat. 100, 33—46.

Preston, F.W., 1962. The canonical distribution of commonness and rarity: Part I. Ecology 43, 185—215. https://doi.org/10.2307/1931976.

Rabosky, D.L., 2013. Diversity-dependence, ecological speciation, and the role of competition in macroevolution. Annu. Rev. Ecol. Evol. Syst. 44, 481—502. https://doi.org/10.1146/annurev-ecolsys-110512-135800.

Rabosky, D.L., Hurlbert, A.H., 2015. Species richness at continental scales is dominated by ecological limits. Am. Nat. 185, 572—583. https://doi.org/10.1086/680850.

Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511623387.

Rubalcaba, J.G., Gouveia, S.F., Villalobos, F., Cruz-Neto, A.P., Castro, M.G., Amado, T.F., Martinez, P.A., Navas, C.A., Dobrovolski, R., Diniz-Filho, J.A.F., Olalla-Tárraga, M.Á., 2022. Physical constraints on thermoregulation and flight drive morphological evolution in bats. Proc. Natl. Acad. Sci. U. S. A. 119, e2103745119. https://doi.org/10.1073/pnas.2103745119.

Ruffley, M., Peterson, K., Week, B., Tank, D.C., Harmon, L.J., 2019. Identifying models of trait-mediated community assembly using random forests and approximate Bayesian computation. Ecol. Evol. https://doi.org/10.1002/ece3.5773.

Silva, D.C., Oliveira, H.F.M., Domingos, F.M.C.B., 2024. Cerrado bat community assembly is determined by both present-day and historical factors. J. Biogeogr. https://doi.org/10.1111/jbi.14798 jbi.14798.

Soberon, J., Peterson, A.T., 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodivers. Inform. 2. https://doi.org/10.17161/bi.v2i0.4.

Stevens, G.C., 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. Am. Nat. 133, 240—256.

Thorson, G., 1936. The larval development, growth, and metabolism of Arctic marine bottom invertebrates compared with those of other seas. Meddelingen Om Grönland 100, 1—155.

Whittaker, R.H., Levin, S.A., Root, R.B., 1973. Niche, habitat, and ecotope. Am. Nat. 107, 321—338. https://doi.org/10.1086/282837.

Whittaker, R.J., Fernández-Palacios, J.M., Matthews, D.T.J., 2007. Island Biogeography: Geo-Environmental Dynamics, Ecology, Evolution, Human Impact, and Conservation. Oxford University Press, Oxford, New York.

Whittaker, R.J., Fernández-Palacios, J.M., Matthews, T.J., Borregaard, M.K., Triantis, K.A., 2017. Island biogeography: taking the long view of nature's laboratories. Science 357, eaam8326. https://doi.org/10.1126/science.aam8326.

Wiens, J.J., Donoghue, M.J., 2004. Historical biogeography, ecology and species richness. Trends Ecol. Evol. 19, 639—644. https://doi.org/10.1016/j.tree.2004.09.011.