

Geographic patterns of biodiversity

by

Fabricio Villalobos and Thiago F. Rangel

Depto. Ecologia, ICB, Universidade Federal de Goiás
Campus II/UFG, CxP 131, 74001-970 Goiânia, Goiás, Brasil

This is a separate chapter from the open access book

Frontiers in Ecology, Evolution and Complexity

Mariana Benítez, Octavio Miramontes & Alfonso Valiente-Banuet (Editors)

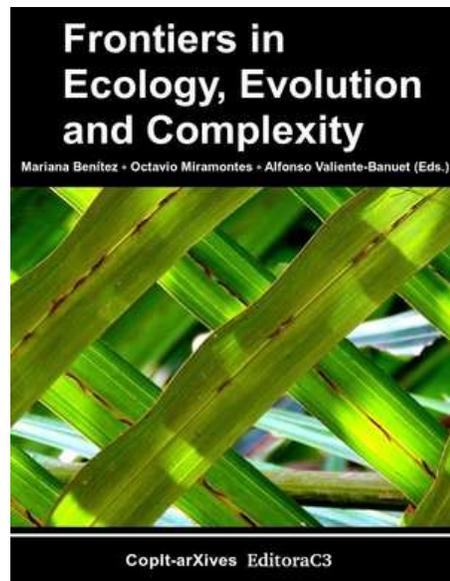
CopIt-arXives, 2014

Mexico City

ISBN: 978-1-938128-05-9

©CopIt-arXives

<http://scifunam.fisica.unam.mx/mir/copit/TS0012EN/TS0012EN.html>



Contents

| | | |
|-----------------------------|--|----------|
| F. Villalobos & T.F. Rangel | Geographic patterns of biodiversity | 1 |
| 1 | Abstract | 1 |
| 2 | Resumen | 1 |
| 3 | Introduction | 2 |
| 4 | Description of patterns and correlations | 3 |
| 5 | Mechanistic theories of biodiversity | 3 |
| 6 | Null and stochastic simulation models | 6 |
| 7 | Bibliography | 9 |

Geographic patterns of biodiversity

F. Villalobos & T.F. Rangel, Universidade Federal de Goiás, Brazil

1 Abstract

Geographic variation in biodiversity is a well-documented natural phenomenon but no satisfactory explanations regarding its origins have yet been reached. The inherent complexity of ecological systems hampers the comprehensive study and understanding of biodiversity patterns. Recent advancements in theoretical and methodological approaches provide means to explicitly deal with such ecological complexity allowing developing and testing specific predictions about potential causal mechanisms. Macroecology is a relatively recent ecological discipline that has emerged as a synthetic research program focused on the emergent, statistical properties of complex ecological systems at broad spatial and temporal scales. Different approaches, from statistical correlations to computer simulations, are employed within macroecology in order to understand biodiversity patterns. Here we provide a brief overview of such macroecological approaches and their relevance for studying the complex phenomenon of biodiversity as expressed over the geography of our planet.

2 Resumen

La variación geográfica de la biodiversidad es un fenómeno natural bien documentado pero del cual aún no se tienen explicaciones satisfactorias. La inherente complejidad de los sistemas ecológicos impide el estudio y comprensión completos de los patrones de biodiversidad. Avances recientes en diferentes enfoques teóricos y metodológicos proveen la posibilidad de lidiar directamente con la complejidad ecológica, permitiendo desarrollar y evaluar predicciones específicas acerca de los potenciales mecanismos causales. La macroecología es una disciplina ecológica relativamente reciente que ha surgido como un programa de investigación sintético enfocado en las propiedades estadísticas y emergentes de sistemas ecológicos complejos en amplias escalas espaciales y temporales. Distintos enfoques, desde correlaciones estadísticas hasta simulaciones por computadora, son empleados por la macroecología para entender los patrones de biodiversidad. Aquí

presentamos una breve descripción y discusión de dichos enfoques macroecológicos y su importancia para estudiar el complejo fenómeno de la biodiversidad y su expresión a lo largo de la geografía de nuestro planeta.

3 Introduction

One of the most intriguing natural phenomena is the variety of species and their heterogeneous distribution over the planet. For instance, most species are distributed along the tropics whereas a smaller fraction of species is distributed over temperate regions, a pattern known as the Latitudinal Diversity Gradient. Such biodiversity gradient is well documented, yet explanations about its causes remain elusive. Explanations for this and other geographic patterns of biodiversity have changed through time and disciplines, with biogeography favoring regional, historical processes –speciation, extinction, dispersal– and ecology favoring local, contemporary processes –mainly biotic interactions. The ecological approach was heavily influenced by the experimental tests of ecological systems, which attempt to take ecological processes apart and study their components separately. However, it has been implicitly recognized that complex ecological systems are not amenable to simple experiments [1].

The processes underlying biodiversity patterns are complex and varied. At local spatial scales, ecological communities vary greatly, imposing challenges to the detection of general patterns and processes that may govern the origin and maintenance of biodiversity [2]. In an attempt to overcome this lack of generalization, a more comprehensive, broad-scale and statistical approach has been proposed to study biodiversity patterns. This approach has been defined as Macroecology [1, 3]. Macroecology introduces a historical and geographical perspective on local, ecological systems and an ecological perspective to understand regional and continental biotas [1]. It applies a statistical mechanics approach with an emphasis on the statistical regularities that emerge from studying large groups species, about which it makes the fewest possible assumptions [4]. The macroecological rationale is based on the assumption that macroscopic patterns of complex ecological systems in space and time are not epiphenomena, thus not reducible to a small set of local components and current processes [5].

The macroecological framework to understand the mechanistic basis of geographic patterns of biodiversity has changed since its original inception, even within the short time that the discipline has been around. From a purely descriptive and correlative methodology to a stochastic simulation and mechanistic modeling approach, macroecology has established itself as major biological research program [6]. Here we provide a brief overview of current macroecological approaches and discuss their relevance for understanding the complex phenomenon of biodiversity at geographic scales.

4 Description of patterns and correlations

Initially, macroecology was mostly occupied with the description of patterns and their explanation under a correlative approach. Studies relying on this approach were limited to the simple evaluation of the concordance between the geographic patterns, mainly species richness variation, and environmental factors, such as temperature, precipitation, and evapotranspiration [7] (Figure 1). The underlying assumption is that species are in equilibrium with climate –existing where climate is favorable– and species richness gradients are driven by contemporary climate. Similar, strong correlations have been described for a varied set of taxa (e.g. animals and plants) over the same or distinct regions, suggesting that such correlative patterns are widespread and, more importantly, underlying mechanisms may be general. For example, [8] found globally consistent strong correlations between angiosperm richness and mean annual temperature and potential evapotranspiration; whereas [9] identified water and energy-related variables (e.g. actual evapotranspiration and plant productivity) as important determinants of both animal and plant species richness. Notwithstanding the generality of such correlations, they fail to inform about the actual processes changing the number of species in an area.

5 Mechanistic theories of biodiversity

Statistical descriptions of ecological attributes represent the core of the macroecological endeavor and the focus of current biodiversity theories. Patterns such as the frequency distributions of abundance, body size, geographic range size, and the correlations between these attributes are of paramount importance to understand the processes underlying its emergence [4]. Frequency distributions of ecological attributes, namely those representing lognormal and power law distributions, are uncannily similar to patterns in physical, geological, economic, and cultural systems [10]. For instance, the frequency distribution of abundances among species in ecological communities has a remarkable similarity with the citation frequencies of scientific papers. Likewise, the relationship between species richness and area –one of the few general rules in ecology– resembles the number of unique words and total word length in texts [10]. These congruent patterns beg for a more universal explanation. Complexity science has explained such patterns as a result of general processes and the multiplicative, rather than additive, interaction of variables within complex systems (e.g. ecological communities) [10]. In ecology, such processes have been related to the dynamics of species at both local and broad spatial scales [5].

The neutral theory of biodiversity (NTB, [11]) provided the first model linking local scale population dynamics with broad scale biodiversity dynamics. This theory is based on a simple set of assumptions: that all organisms of all species have identical ecological properties and that local communities are saturated with no changes in the total number of individuals occurring over time (i.e. “zero-sum” dynamics). Under NTB, diversity

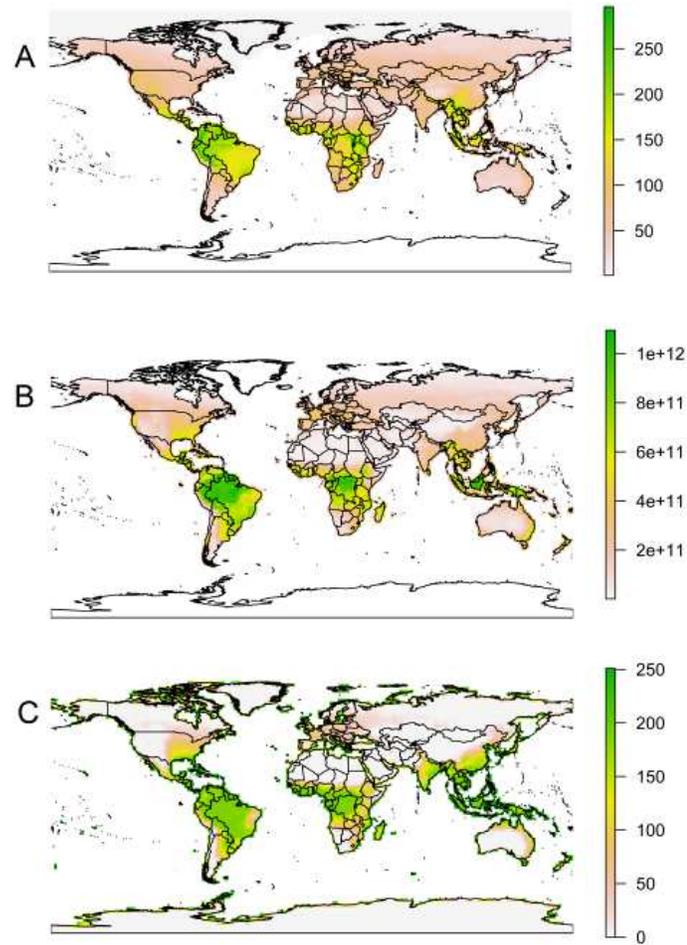


Figure 1: (A) Map depicting the species richness of mammals in the world. (B) Map showing the variation in Net Primary Productivity (NPP; units are in mass of carbon per unit area per year ($gCm^{-2}yr^{-1}$)). (C) Map showing the variation in Actual Evapotranspiration (AET; $mmyr^{-1}$). Note that all three variables (species richness, NPP and AET) show higher values in the Tropics.

is generated and maintained by stochastic birth, death and immigration processes [11]. Neutral theory predictions have remarkably reproduced biodiversity patterns such as the species-abundance distribution in local communities. Furthermore, NTB makes additional testable predictions such as species-area relationships, population and community dynamics, and phylogenetic tree shape and branch lengths, thus linking locally and contemporary to broader and historical spatial and temporal scales. In this sense, NTB continues to play an important role in biodiversity research by providing quantitative and process-based null hypotheses against which macroecological patterns can be contrasted.

Another relevant biodiversity theory is the metabolic theory of ecology (MTE) [12]. This theory relies on first principles of physics, chemistry and biology to predict ecological properties of populations, communities and ecosystems from organisms' metabolic rates [12]. MTE predicts a mass-temperature dependence of biological processes that integrates cellular to global-level processes based on the well-known scaling law between metabolic rate and body size in which the whole-organism metabolic rate, I , scales as $I = I_o M^{3/4}$ (where I_o is a normalization constant and M is the body mass). For instance, a proposed MTE model predicts that when temperature scales as $1/kT$ (where T is temperature in Kelvin and k is the Boltzmann's constant of $8.62 \times 10^{-5} eV K^{-1}$) the logarithm of species richness should be linear with slope between -0.6 and -0.7 , thus species richness increasing with temperature [13]. MTE has provided interesting explanations of biodiversity patterns linking temperature, metabolic biochemistry, physiology, and evolutionary rates. [14], for example, developed a model of kinetic energy that successfully predicted rates of genetic divergence and speciation in planktonic foraminifera as increasing toward tropical latitudes. Further improvements to the MTE are expected, including testing its foundations and assumptions. As such, MTE is far from complete but efforts are being conducted to formalize and test the essential roles of body size, metabolism, and temperature. In sum, MTE represents a fundamental advancement linking biodiversity patterns to basic biological principles influenced by the environment and should still prove useful in theoretical and applied terms for understanding biodiversity.

A more recent biodiversity theory aimed at predicting scaling metrics such as the species-area and species-abundance relationships, and the species-level occupancy distributions across space is the Maximum Entropy (MaxEnt) theory [15]. MaxEnt is based on maximizing information entropy –a measure of the lack of structure or detail in the probability distribution describing a knowledge system– to infer such macroecological metrics. MaxEnt aims to describe the central tendencies observed for the entire range of macroecological metrics of interest without adjusting parameters or prejudging what is driving the system [15]. This approach is based on state variables, which are properties of a system that comprise the conditions whose specification is necessary to implement theory but whose determination lies outside the theory. In macroecology, these state variables can be defined as the area of the system, the number of species in that area, the total number of individuals in those species, and the total rate of metabolic energy consumed by those individuals [15]. Contrasting with the neutral and metabolic theories, MaxEnt

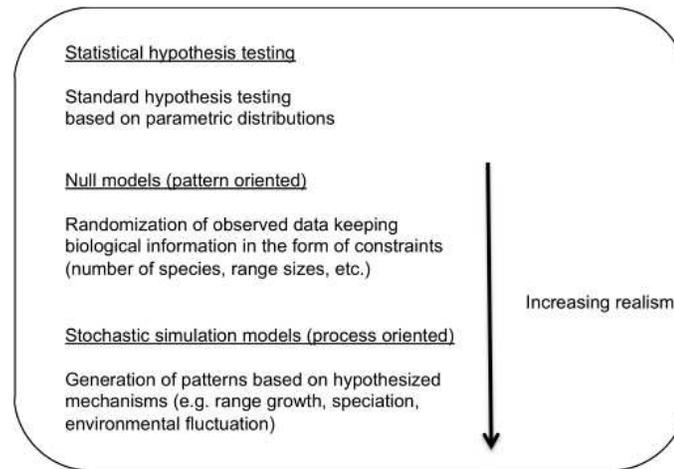


Figure 2: Conceptual description highlighting differences among statistical hypothesis testing, standard null models and stochastic simulation models (based on [19]).

theory has yet to be widely applied and tested.

The above theories rely on the statistical description of observed patterns without invoking the multiple interactions among different ecological mechanisms or, in the case of MTE and MaxEnt, without considering stochasticity and contingency of species spatial and temporal dynamics. Indeed, this is one of the great advantages of such null theories [16]. These theories can be informative when succeed as well as when they fail. For instance, success of the theory means that mechanisms incorporated into the parameters' values are sufficient to explain patterns. Conversely, when failure, the theory tells us that more mechanistic information than that captured by its parameters is needed to predict patterns [16]. Alternatively, the goal of including explicit mechanistic processes and tracking their dynamics over space and time has been the focus of recent theoretical developments based on computer simulation models.

6 Null and stochastic simulation models

Traditional approaches for understanding biodiversity patterns have relied on small-scale experiments or on fitting simple statistical models to macroecological data. More recently, computer simulation models have emerged as an important alternative to traditional macroecological approaches [17]. These simulation models can be considered as experimental systems and used to mimic biodiversity in a way that can be manipulated, thus helping to develop and test theories about its origin, maintenance and dynamics [18].

Early efforts in simulation modeling were based on the application of null models that include the action of stochastic processes and the possibility of no ecological effect.

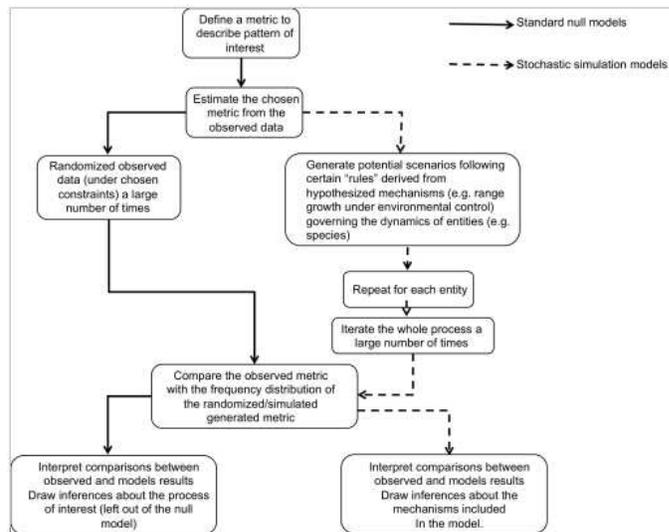


Figure 3: Flow chart illustrating the general protocol for conducting and testing null (solid line) and stochastic simulation models (dashed line) (based on [19]).

Such null models generate expected statistical distributions of the variable of interest from stochastic models based on biological theory and Monte Carlo methods (i.e. keeping biological information; species richness or distribution, while randomizing the data) [20] (Figure 2). The interpretation of null models based on their “falseability” and, thus, in the relevance of excluded variables has been and is still valid and important in biogeography, ecology, and macroecology. For instance, much has been learned from the application of null models in the fields of ecology, biogeography, and evolution, with its paramount influence in testing ecological theory in the debate of competition versus stochasticity in determining community structure as an example [20]. In macroecology, null models have been regularly applied with different procedures simulating null scenarios being implemented, especially when testing species richness gradients and coexistence patterns [21, 22]. Nevertheless, the growing interest in considering specific mechanisms beyond the randomization of data together with the availability of greater computational capacity has led to more sophisticated null and mechanistic models (Figures 2 and 3).

Geographic variation in species richness is ultimately determined by the differential coexistence of species in distinct regions of the globe, resulting from the overlap of species ranges differing in size, shape, and location. Thus, current macroecological approaches advocate the stochastic simulation of species’ range building and placement to study geographic patterns of biodiversity [17]. These simulation models started with the now classic Mid-Domain Effect (MDE), which examined the effect of geometric constraints imposed by hard boundaries on the distribution of species, and consequently on

emerging patterns of species richness [23]. Initial MDE models simulated ranges within a homogeneous, one-dimensional domain of regular shape [23] or resembling actual two-dimensional continents [24]. More recently, climatic and topographic gradients have been included in spatially explicit simulations as well as evolutionary dynamics such as speciation, extinction, dispersal, and niche conservatism/evolution [25], thus directly including ecological and evolutionary mechanisms into the modeling framework.

Simulation models differ from statistical models such as the correlative models or some of the mechanistic theories outlined above. These latter, parameter-fitting methods are usually developed to predict rather than explain biodiversity patterns. Conversely, simulation models are built to offer an explanation of biodiversity patterns [18]. Indeed, great conceptual advancements have been reached by applying simulation models to comprehend the causes of biodiversity patterns. For instance, the explicit consideration of first principles thought to govern the origin and geographic spread of species has highlighted the interplay among evolutionary dynamics, ecological processes, and environmental conditions in effectively driving biodiversity patterns [17]. In a seminal contribution, [25] developed a simulation model incorporating ecological and evolutionary “mechanisms” such as climatic fluctuation, species’ environmental preferences and evolution, as well as formation of new species by speciation. They found that the species richness pattern for the Birds of South America could be closely reproduced by a combination of species origin within the Tropics and strong niche conservatism [25]. In a less dynamic framework but similarly informed model, [26] showed that climatic conditions along the geographic domain as well as inheritance of niche preferences among species are important but not enough to explain similarity among sites and species in the bat family Phyllostomidae. Instead, other, additional causes such as historical processes are needed to explain the observed patterns in that important bat family.

Stochastic simulation models represent one of the most important methods in biogeography and macroecology [27], allowing the exploration of specific hypotheses and predictions that otherwise would be impossible [18]. Further developments are still required to understand biodiversity patterns and evaluate the usefulness of simulation models, some of which are well on their way. For instance, applying a “virtual ecologist approach” [28] to evaluate simulation models against known virtual data can help to assess the model’s capacity to discern underlying processes. Also, the consideration of composite response variables and patterns beyond species richness (e.g. co-diversity among sites in terms of shared species and co-distribution among species in terms of overlapping geographical distributions [26]) can be used to validate models at different hierarchical levels [29] and provide stronger tests of potential mechanisms.

Geographic patterns of biodiversity are a complex natural phenomenon requiring advanced methodologies to comprehend their causes. Macroecology has come a long way in providing a synthetic framework for broad-scale biodiversity patterns, linking different disciplines and introducing novel methods. More recently, it has expanded its focus and now routinely considers larger temporal scales, including phylogenetic and paleoclimatic

information to allow a deep-time perspective on biodiversity patterns. Despite increasing documentation of empirical patterns and significant conceptual and methodological advances, we are still far from explaining biodiversity patterns. Several challenges remain to be solved in order to accomplish this objective. Among others, the paucity of good data (e.g. standardized sampling schemes at different spatial scales, information on species traits, phylogeny and behavior) continues to be a problem even for well-known taxa such as vertebrates. In addition, better methods are still needed to deal with data biases, uncertainty assessment, and correlations among hierarchical predictors [6], as well as procedures for model testing and dealing with more informative response variables or patterns [17]. This being recognized, the discipline of macroecology will certainly continue to expand and contribute towards the overarching goal of generating a unifying theory of biodiversity.

The macroecological programme currently integrates varied and sophisticated approaches aimed at understanding biodiversity patterns. Of these, simulation models hold great promise to represent and understand the inherent complexity of ecological systems as well as anticipating potential scenarios for biological conservation under natural and anthropogenic disturbances such as the current biodiversity crisis and climate change. Macroecological approaches thus offer promise and fruitful means to explicitly deal with ecological complexity and provide a more comprehensive understanding of biodiversity patterns at broad spatial and temporal scales.

7 Bibliography

- [1] J. H. Brown, *Macroecology*. University of Chicago Press, 1995.
- [2] J. H. Lawton, "Are there general laws in ecology?" *Oikos*, vol. 84, no. 2, pp. 177–192, 1999.
- [3] J. H. Brown and B. A. Maurer, "Macroecology: the division of food and space among species on continents," *Science*, vol. 243, no. 4895, pp. 1145–1150, 1989.
- [4] P. A. Marquet, "Macroecological perspectives on communities and ecosystems," *The Princeton guide to ecology*, p. 386, 2009.
- [5] B. A. Maurer, *Untangling ecological complexity: the macroscopic perspective*. University of Chicago Press, 1999.
- [6] J. Beck, L. Ballesteros-Mejia, C. M. Buchmann, J. Dengler, S. A. Fritz, B. Gruber, C. Hof, F. Jansen, S. Knapp, H. Kreft *et al.*, "What's on the horizon for macroecology?" *Ecography*, vol. 35, no. 8, pp. 673–683, 2012.
- [7] K. J. Gaston, "Global patterns in biodiversity," *Nature*, vol. 405, no. 6783, pp. 220–227, 2000.

- [8] A. P. Francis and D. J. Currie, "A globally consistent richness-climate relationship for angiosperms," *The American Naturalist*, vol. 161, no. 4, pp. 523–536, 2003.
- [9] B. A. Hawkins, R. Field, H. V. Cornell, D. J. Currie, J.-F. Guégan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien *et al.*, "Energy, water, and broad-scale geographic patterns of species richness," *Ecology*, vol. 84, no. 12, pp. 3105–3117, 2003.
- [10] J. C. Nekola and J. H. Brown, "The wealth of species: ecological communities, complex systems and the legacy of frank preston," *Ecology Letters*, vol. 10, no. 3, pp. 188–196, 2007.
- [11] S. P. Hubbell, *The unified neutral theory of biodiversity and biogeography (MPB-32)*. Princeton University Press, 2001.
- [12] J. H. Brown, J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West, "Toward a metabolic theory of ecology," *Ecology*, vol. 85, no. 7, pp. 1771–1789, 2004.
- [13] A. P. Allen, J. H. Brown, and J. F. Gillooly, "Global biodiversity, biochemical kinetics, and the energetic-equivalence rule," *Science*, vol. 297, no. 5586, pp. 1545–1548, 2002.
- [14] A. P. Allen, J. F. Gillooly, V. M. Savage, and J. H. Brown, "Kinetic effects of temperature on rates of genetic divergence and speciation," *Proceedings of the National Academy of Sciences*, vol. 103, no. 24, pp. 9130–9135, 2006.
- [15] J. Harte, *Maximum entropy and ecology: a theory of abundance, distribution, and energetics*. Oxford University Press, 2011.
- [16] ———, "The value of null theories in ecology," *Ecology*, vol. 85, no. 7, pp. 1792–1794, 2004.
- [17] N. J. Gotelli, M. J. Anderson, H. T. Arita, A. Chao, R. K. Colwell, S. R. Connolly, D. J. Currie, R. R. Dunn, G. R. Graves, J. L. Green *et al.*, "Patterns and causes of species richness: a general simulation model for macroecology," *Ecology Letters*, vol. 12, no. 9, pp. 873–886, 2009.
- [18] S. L. Peck, "Simulation as experiment: a philosophical reassessment for biological modeling," *Trends in Ecology & Evolution*, vol. 19, no. 10, pp. 530–534, 2004.
- [19] N. J. Gotelli and W. Ulrich, "Statistical challenges in null model analysis," *Oikos*, vol. 121, no. 2, pp. 171–180, 2012.
- [20] N. J. Gotelli and G. R. Graves, *Null models in ecology*. Smithsonian Institution, 1996.

- [21] H. T. Arita and E. Vázquez-Domínguez, "The tropics: cradle, museum or casino? a dynamic null model for latitudinal gradients of species diversity," *Ecology Letters*, vol. 11, no. 7, pp. 653–663, 2008.
- [22] F. Villalobos and H. T. Arita, "The diversity field of new world leaf-nosed bats (phyllostomidae)," *Global Ecology and Biogeography*, vol. 19, no. 2, pp. 200–211, 2010.
- [23] R. K. Colwell and D. C. Lees, "The mid-domain effect: geometric constraints on the geography of species richness," *Trends in Ecology & Evolution*, vol. 15, no. 2, pp. 70–76, 2000.
- [24] W. Jetz and C. Rahbek, "Geometric constraints explain much of the species richness pattern in African birds," *Proceedings of the National Academy of Sciences*, vol. 98, no. 10, pp. 5661–5666, 2001.
- [25] T. F. L. Rangel, J. A. F. Diniz-Filho, and R. K. Colwell, "Species richness and evolutionary niche dynamics: a spatial pattern-oriented simulation experiment," *The American Naturalist*, vol. 170, no. 4, pp. 602–616, 2007.
- [26] F. Villalobos, A. Lira-Noriega, J. Soberon, and H. T. Arita, "Co-diversity and co-distribution in Phyllostomid bats: Evaluating the relative roles of climate and niche conservatism," *Basic and Applied Ecology*, vol. 15, no. 1, pp. 85–91, 2014.
- [27] T. F. Rangel and J. A. F. Diniz-Filho, "Biogeographical models," in *Encyclopedia of Biodiversity 2nd ed.*, S. Levin, Ed. Waltham, MA: Academic Press, 2013, vol. 1, pp. 565–575.
- [28] D. Zurell, U. Berger, J. S. Cabral, F. Jeltsch, C. N. Meynard, T. Münkemüller, N. Nehrbass, J. Pagel, B. Reineking, B. Schröder *et al.*, "The virtual ecologist approach: simulating data and observers," *Oikos*, vol. 119, no. 4, pp. 622–635, 2010.
- [29] V. Grimm, E. Revilla, U. Berger, F. Jeltsch, W. M. Mooij, S. F. Railsback, H.-H. Thulke, J. Weiner, T. Wiegand, and D. L. DeAngelis, "Pattern-oriented modeling of agent-based complex systems: lessons from ecology," *Science*, vol. 310, no. 5750, pp. 987–991, 2005.