

MACROECOLOGY

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Summary

The aim Ecology is to understand patterns of distribution and abundance of organisms on Earth, as well as the underlying mechanisms responsible for the origin and maintenance of these patterns. Macroecology is a field of ecology characterized by a statistical investigation of the relationship between the dynamics and interactions of species populations that have been studied on small scales by ecologists and processes of speciation, extinction and expansion and contraction of ranges that have been investigated on much larger scales by biogeographers, paleontologists and macroevolutionists. In this chapter we describe the main aspects of the modern macroecology research program, focusing on the main scientific problems evaluated by this research field. We also emphasize why tropical regions are challenging to macroecological studies and, although macroecology is still in its infancy, hopefully it will allow a deeper understanding of patterns and processes of biological diversity and provides the theoretical basis for developing efficient broad-scale conservation strategies.

1. Introduction

The main purpose of ecology is to understand patterns of distribution and abundance of organisms on Earth, and the underlying mechanisms responsible for these patterns. However, given the high complexity of ecological system, many different (but not mutually exclusive) approaches have been used to study these systems since early XX

century, and one of the main dichotomies is related to geographical and evolutionary scales. Most of classical approaches in Ecology, derived from basic demographic and population dynamic equations (e.g., Lotka-Volterra equations), were developed at spatial and temporal local scales, and eventually projected to larger scales. On the other hand, it is possible to follow an opposite path and study the overall patterns at broad scales, without paying attention to details at local scales (e.g., equilibrium theory of island biogeography). These opposite approaches co-existed for a while in ecology, only in the second half of the XX century recently they started to be fused in the new context of macroecology.

The term “Macroecology” was proposed by James Brown and Brian Maurer in 1989, in a paper published in *Science*, and they define it as “...a non-experimental, statistical investigation of the relationship between the dynamics and interactions of species populations that have been studied on small scales by ecologists and processes of speciation, extinction and expansion and contraction of ranges that have been investigated on much larger scales by biogeographers, paleontologists and macroevolutionists”.

More recently, in the late 1990's decade, it has been argued that macroecology also can be understood as the analysis of a large number of “ecological particles”, so that the research program should focus on the “...statistical distribution of variables among large collections of equivalent, but not identical, units, such as individual organisms within species or species within communities or biogeographic regions”. Thus, because of the broad scale issues involved, macroecology can be viewed now as a unifying conceptual and methodological framework for understanding patterns of abundance and distribution, incorporating advances from a wide range of areas of scientific knowledge, including ecology, biogeography, evolutionary biology, population genetics, and physiology.

The number of studies in macroecology increased exponentially since the early 1990's (Figure 1), although it is in fact difficult to evaluate the growth of this integrative framework based on a simple scientometric search. Since macroecology develops upon a series of previous and now classical studies in community ecology from 1960's-1970's, it encompasses now different research lines. Indeed, although the definition formulated in 1989 for the field was a somewhat restrictive, the macroecology research program was later naturally expanded to incorporate many other classical research areas from community ecology and biogeography, including the species-area relationships, latitudinal diversity gradients, island biogeography and ecogeographical patterns, such as Bergmann's rule. Thus, there is now a high heterogeneity in the research programs associated with the term macroecology.

The heterogeneity in the macroecology research program and the old history of investigation of some of the patterns, as well as the multiplicity of patterns and potential underlying ecological mechanisms behind them, led to the development of attempts to unify the field from first principles. Examples include J. H. Brown's new metabolic theory of ecology, B. McGill and C. Collins' unified principles based on the relationship between abundance and distribution and Price's fusion of macroecology and evolution. At the same time, it is important to be caution about linking patterns and processes,

since neutral and null dynamics can also generate macroecological structures, as pointed out by G. Bell.

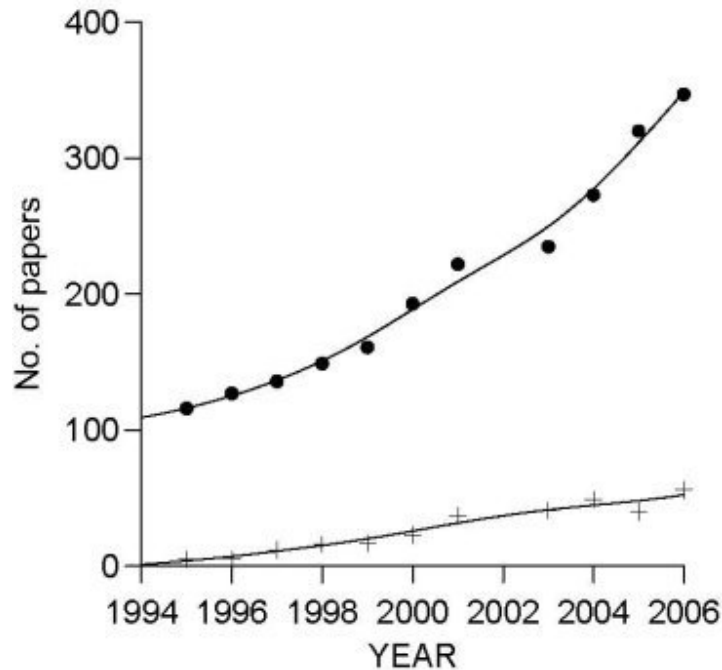


Figure 1. Increase in the number of published papers per year indexed in Thomson Instituto (Web of Science) between 1995 and 2006, using “macroecology” as a keyword (+) and using a more general definition, and using the terms "macroecology", "geographic range", "latitudinal gradients", “species-area relationship” "Bergmann's rule", as simultaneous keywords (●).

Although the current macroecology research program is clearly based on these early developments, it is important to stress the differences between the original studies and their “modern” counterparts. It is beyond the scope of this paper to review each detail of these studies, but it is possible to recognize general trends towards more processes-based approaches, under a more mechanistic basis (or at least a deeper attempt to achieve this mechanistic basis). These advances were possible both because of a clearer understanding of the theoretical basis ecological systems dynamics and due to advances in data analysis and acquisition at broad spatial and temporal scales. At the same time, it is important to consider that attempts to unify patterns and processes should take into account the multiple and hierarchical components due to variations in spatial and temporal scales (see the excellent papers by R. J. Whittaker and colleagues, T. Blackburn and K. Gaston, and C. Rahbek, on this subject). At the same time, biodiversity crisis forced ecologists to study systems at broader scales, in an attempt to solve conservation problems at regional, national and global spatial scales.

Besides providing significant information to ecology development as a whole, studying patterns in the individuals and species distributions across space have also contributed to decipher the forces that structure and maintain biodiversity. Such improvement in the theoretical framework shows important practical applications in management and conservation of biodiversity. We can highlight, for example, better predictions of

species extinction rates or vulnerability levels under perturbations, at regional scales. On the other hand, it will also help to understand properly biological invasions under the perspectives of both invasive species and also invaded habitats. Moreover, this macroecological approach can also allow more effective land protection policies, the design of more efficient and accurate census strategies, and more effective estimates of species richness from sparse census data. Finally, it will likely to contribute to our predictions about how global climate changes will disturb current biodiversity patterns, as pointed out by M. B. Araújo and C. Rahbek in 2006, and by J. Kerr and colleagues in 2007.

Here we describe the main current aspects of the macroecology research program, mainly in terms of the main scientific problems evaluated by this research field. We also emphasize why tropical regions are challenging to macroecological studies. The macroecology research program it is still in its infancy, but hopefully it will allow a deeper understanding of patterns and processes of life on Earth and provides the theoretical basis for developing efficient broad-scale conservation strategies.

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Bibliography

Araújo, M.B. and C. Rahbek (2006). How does climate change affect biodiversity? *Science*, 313, 1396-1397. [A new perspective for predicting future species distributions under climate changes from the bioclimate models that were recently architected and tested to estimate current species ranges.]

Beck, J., I.J. Kitching and E.K. Linsenmair (2006). Extending the study of range–abundance relations to tropical insects: sphingid moths in Southeast Asia. *Evolutionary Ecology Research*, 8, 677-690. [An example of the interspecific Range-Abundance Relationship in tropical insects].

Bell, G. (2001). Neutral macroecology. *Science*, 293, 2413-2418. [An attempt to explain macroecological patterns under neutral dynamics].

Bini, L.M., J.A.F. Diniz, T. Rangel, R.P. Bastos and M.P. Pinto (2006). Challenging Wallacean and Linnean shortfalls: knowledge gradients and conservation planning in a biodiversity hotspot. *Diversity and Distributions*, 12, 475-482. [An original approach to solve biodiversity and conservation problems in a poorly know and highly rich neotropical biome].

Blackburn, T.M., P. Cassey and K.J. Gaston (2006). Variations on a theme: sources of heterogeneity in the form of the interspecific relationship between abundance and distribution. *Journal of Animal Ecology*, 75, 1426-1439. [A comprehensive review of interspecific Range-Abundance Relationship].

Blackburn, T.M. and K.J. Gaston eds. (2003) *Macroecology: concepts and consequences*. Blackwell Scientific Publications, Oxford. [A review of the main research lines in macroecology, covered in the first international meeting about this topic].

Blackburn, T.M. and K.J. Gaston (2002). Scale in macroecology. *Global Ecology and Biogeography*, 11,

185-189. [An overview of effects of scale in macroecology].

Brown, J.H. (1995). *Macroecology*. University of Chicago Press: Chicago. [The first text book in macroecology].

Brown, J. H. and B. A. Maurer (1987). Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. *The American Naturalist*, 130, 1-17. [One of the first papers in macroecology, in which the patterns of constraint envelope between body size, geographic range size and abundance are described].

Brown, J. H. and B. A. Maurer (1989). Macroecology: the division of food and space among species on continents. *Science*, 243,1145-1150. [The paper that launched the term “macroecology”].

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage and G. B. West (2004). Toward a metabolic theory of ecology. *Ecology* 85, 1771-1789. [A synthesis of the developing metabolic theory of ecology. See, also the paper by Hawkins and colleagues published in *Ecology* in, 2007 (in press), criticizing the application of a particular model from metabolic theory to the studies of diversity gradients]

Colwell, R.K. and D.C. Lees (2000). The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution*, 15, 70-76. [The first presentation and overview on geometric models explaining species richness patterns, the mid-domain effect].

Currie, D.J., G.G. Mittelbach, H.V. Cornell, R. Field., J.F. Guégan, B.A. Hawkins, D.M. Kaufman, J.T. Kerr, T. Oberdorff, E. O'Brien and J.R.G. Turner (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121-1134. [An interesting examination of some relevant hypothesis to explain climate-richness relationship, under a hypothetical-deductive theoretical framework].

Diniz-Filho, J. A. F. (2004). Macroecology and the hierarchical expansion of evolutionary theory. *Global Ecology and Biogeography* 13, 1-5. [A discussion on how the hierarchical expansion of evolutionary theory and adaptive processes at higher taxonomic levels, such as species selection and sorting, could create macroecological patterns, mainly the relationship between geographic range and abundance].

Diniz-Filho, J.A.F., L.M. Bini, M.A. Rodríguez, T.F.L.V.B. Rangel and B.A. Hawkins (2007). Seeing the forest for the trees: partitioning ecological and phylogenetic components of Bergmann's rule in European Carnivora. *Ecography*, 30, in press. [A new analytical framework that allows a more integrative explanation for a widely known macroecological patterns such as geographic variation in body size, decoupling them into historical and ecological components].

Elith, J., C.H. Graham, R.P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R.J. Hijmans, F. Huettmann, J.R. Leathwick, A. Lehmann, J. Li, L.G. Lohmann, B.A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J.McC.M. Overton, A.T. Peterson, S.J. Phillips, K. Richardson, R. Scachetti-Pereira, R.E. Schapire, J. Soberón, S. Williams, M.S. Wisz and N.E. Zimmermann (2006). Novel methods improve prediction of species' distributions from occurrence data. - *Ecography* 29: 129-151. [A comparative evaluation of many methods currently available for species' niche modeling].

Gaston, K. and T. Blackburn (2000). *Pattern and Process in Macroecology*. Blackwell Science: London. [A standard text-book on Macroecology].

Gaston, K.J. and J.H. Lawton (1998). Patterns in Body Size, Population Dynamics, and Regional Distribution of Bracken Herbivores. *The American Naturalist*, 132, 662-680. [A classical review that by investigating correlates between local population variables, have determined community patterns in a “bottle up” approach].

Gaston, K.J. (2003). *The structure and dynamics of geographic ranges*. Oxford University Press: Oxford. [A comprehensive overview of species' geographic range patterns and processes].

Gotelli, N. J. and B. J. McGill (2006). Null versus neutral models: what's the difference? *Ecography*, 29, 793-800. [An extremely enlightening explanation on these often confounded concepts].

Graham, C. H. and R. J. Hijmans (2006). A comparison of methods for mapping species ranges and species richness. *Global Ecology and Biogeography*, 15, 578-587. [A comparison of methods of niche modeling and their effect on estimating richness patterns].

Hawkins, B.A., R Field, H V. Cornell, D J. Currie, J F. Guegan, D M. Kaufman, J T. Kerr, G G.

Mittelbach, T Oberdorff, E M. O'Brien, E E. Porter and JRG Turner . (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105-3117. [A meta-analytical approach synthesizing the effects of climate on species richness, highlighting the mechanisms associated with water-energy dynamics].

Hawkins, B. A., Diniz-Filho, J. A. F., C. Jaramillo and S. A. Soeller (2007). Climate, niche conservatism and global bird diversity gradient. *The American Naturalist*, 170 (supplement), S16-S27. [A paper supporting that niche conservatism and time-for-speciation hypotheses explain well the latitudinal diversity gradient on bird species].

Hubbell, S.P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press: Princeton. [A book that introduces one of the most important current theories in ecology].

Kerr, J. T., H. Kharouba and D. J. Currie. 2007. The macroecological contribution to global change solutions. *Science*, 316, 1581-1584. [An account of the potential contributions of macroecology research program to the studies in global changes]

Lomolino, M.V. and L.R. Heaney eds. (2004) *Frontiers of biogeography*. Sinauer Associates, Sunderland. [A review of the main research lines in biogeography, covered in the first meeting of the International Biogeographical Society].

Lomolino, M.V., B.R. Riddle and J.H. Brown (2005). *Biogeography, 3rd edn*. Sinauer Associates: Sunderland. [a standard text-book on Biogeography].

Lomolino, M.V., D.F. Sax and J.H. Brown (2004). *Foundations of biogeography*. University of Chicago Press: Chicago. [A compilation of "classical" papers and studies in Biogeography]

MacArthur, R.H. (1972). *Geographical Ecology*. Harper and Row: New York. [A classical study of geographical components of ecology, one of the precursors of spatial analysis in ecology and macroecology]

Mace, G., J.L. Gittleman and A. Purvis (2005). Preserving the tree of life. *Science*, 300, 1707:1709. [An excellent overall discussion and presentation of the basic ideas on phylogenetic diversity].

Maurer, B.A. (1999). *Untangling ecological complexity: the macroscopic perspective*. University of Chicago Press: Chicago. [A general overview of broad-scale ecology, with a successful attempt to unify the entire field].

McGill, B. and C. Collins (2003). A unified theory for macroecology based on spatial patterns of abundance. *Evolutionary Ecology Research*, 5, 469-492. [An attempt to unify many different macroecological patterns based on the spatial distribution of abundance of multiple species].

Mittelbach, G.G., D.W. Schemske, H.V. Cornell, A.P. Allen, J.M. Brown, M.B. Bush, S.P. Harrison, A.H. Hurlbert, N. Knowlton, H.A. Lessios, C.M. McCain, A.R. McCune, L.A. McDade, M.A. McPeck, T.J. Near, T.D. Price, R.E. Ricklefs, K. Roy, D.F. Sax, D. Schluter, J. M. Sobel and M. Turelli (2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, 10, 315-331. [A good review of the relevant hypotheses to explain latitudinal gradients of biodiversity, emphasizing the evolutionary and historical explanations].

O'Brien, E.M. (2006). Biological relativity to water-energy dynamics. *Journal of Biogeography*, 33, 1868-1888. [A review of the hypothesis that attempts to explain geography and evolution of life's diversity by the combined effects of availability of water and energy].

Price, P.W. (2003). *Macroevolutionary theory on macroecological patterns*. Cambridge University Press: Cambridge. [One of the first overall attempts to unify macroecology and macroevolution].

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, 8, 224–239. [An excellent account of the effects of spatial scale on the ecological and evolutionary factors driving species richness patterns].

Rangel, T. and J.A.F. Diniz-Filho (2005). Neutral community dynamics, the mid-domain effect and spatial patterns in species richness. *Ecology Letters*, 8, 783-790. [A simulation study that has suggested that neutral theory may provide a mechanistic population level basis for mid-domain effect].

Rangel, T. F. L. V. B., J. A. F. Diniz-Filho and R. K. Colwell (2007). Species richness and evolutionary niche dynamics: a spatial pattern-oriented simulation experiment. *The American Naturalist*, 170 (October)

(in press). [A comprehensive simulation of broad scale patterns of south American bird richness showing that these patterns can be well explained by the balance between niche conservatism and evolution throughout evolutionary time].

Ricklefs, R.E. (2006). Evolutionary diversification and the origin of the diversity-environment relationship. *Ecology*, 87, S3-S13. [An excellent review on evolution of diversity with an integrative perspective based on a macroecological and biogeographical approach].

Sechrest, W., T.M. Brooks, G.A.B. Fonseca, W.R. Konstant, R. A. Mittermeier, A. Purvis, A.B. Rylands and J.L. Gittleman <http://www.pnas.org/content/99/4/2067.abstract> - fn-1(2002). Hotspots and the conservation of evolutionary history. *Proceedings of National Academy of Science USA*, 99, 2067-2091. [An application of the new concepts on phylogenetic diversity to evaluate the biodiversity hotspots].

Siqueira, T., F.O. Roque and S. Trivinho-Strixino (2007). Species richness, abundance, and body size relationships from a neotropical chironomid assemblage: Looking for patterns. *Basic and Applied Ecology*, in press. [An example of analysis of the body size distribution in a tropical insect assemblage].

White, P.E., S.K.M. Ernest, A.J.K. Andrew J. Kerkhoff and B.E. Enquist (2007). Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution*, 22, 323-330. [A good overview on size abundance relationship, including sound guidelines to achieve a synthetic understanding of this pattern].

Whittaker, R. J., K. J. Willis and R. Field (2001). Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, 28, 453-470. [An excellent analysis of how patterns in species richness and diversity should be analyzed in an hierarchical context, and how different factors should be considered in awareness of spatial and temporal scales].

Biographical Sketches

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