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commentary / book review

Island Biogeography: Paradigm Lost?

The Theory of Island Biogeography Revisited, ed. by Jonathan B. Losos and Robert E. Ricklefs
Princeton University Press, 2009, 476 pp. ISBN 978-0-691-13652-3

<http://press.princeton.edu/>

It is axiomatic that we can answer only those questions that we ask, and paradigm shifts in any field of study often consist of dramatic changes in perspective that facilitate the emergence of a large number of new questions. This simple definition certainly describes the impact “The Theory of Island Biogeography” (MacArthur and Wilson, 1967) had on ecology and biogeography. In a matter of a few years, a largely descriptive, non-quantitative, historically-oriented approach was largely supplanted by one that was quantitative and hypothesis-testing, and heavily influenced by a single, visually simple, conceptually intriguing ecological model - the iconic equilibrium model. Its strong emphasis on the impact of varying rates of colonization and extinction on species richness, and the implied levels of turnover in community composition, led quickly to the development of quantitative ecological models that were applied not only to islands but to island-like habitats and habitat fragments, contributing greatly to the early development of conservation biology. These perspectives and insights continue to ramify, leading ever further into broader and broader aspects of ecology and evolution, with no end apparent. In hindsight, it seems that MacArthur and Wilson’s 1967 book, and the earlier but less influential 1963 paper, mark the boundary of an epic sea-change: there is biogeography before the equilibrium model, and there is biogeography after the model.

Or so it would seem, and so it is viewed by some of the authors who participated in the conference held in 2007 that celebrated the contributions of MacArthur and Wilson’s book and the paradigm shift it brought about, which led to the edited volume that is the subject of this review. But this narrative is certainly too simple in several ways.

Perhaps it is inevitable that when a powerful new idea becomes widely accepted and forms

the basis of a dominant conceptual paradigm, it becomes iconic - a symbol of a world-view, a way of placing all new information into a single framework. In the case of MacArthur and Wilson’s book, it was not the volume in its entirety that became iconic so much as one specific component, one very specific graph - the crossed, curving lines of the equilibrium model of island biogeography. For many researchers, that one graph *became* the MacArthur and Wilson theory, and gradually most other parts of the book were forgotten. And in the effort to test, refine, and apply the implications of those two curving lines, sometimes blinders came into existence, causing application of the theory to be limited only to those questions that arose from equilibrium model and the assumptions on which it relies.

These two viewpoints - MacArthur and Wilson’s theory as the well-spring of broad and continuing conceptual insights, and the equilibrium model as constraining blinders that have inhibited the development of new questions and entirely new insights - are polar ends of a spectrum of attitudes that are implicit or explicit in all of the 16 chapters that make up the new volume that celebrates 40 years of research in the MacArthur - Wilson paradigm. It is the breadth of world-views in the chapters that, for me, made the book a fascinating array of ways of viewing biogeography and its place in science, and the place of the 1967 book in biogeography. Perhaps more than anything else, this edited volume makes it clear that biogeography and MacArthur and Wilson’s view of biogeography are not the same thing.

Some of the differences in perspective are immediately apparent in the way the new book is introduced. The brief foreword, by Robert May, describes the 1967 book as a seminal contribution to theoretical ecology, and specifically to community ecology, to the extent that he uses the words “island” and biogeography” only in reference to

the title of MacArthur & Wilson's book. In contrast, the Preface by Losos and Ricklefs also emphasizes the role of the 1967 book in the transition from descriptive to analytical approaches, but they explicitly emphasize islands, biogeography, and the changing conceptualization of the dynamics of island biotas.

It is to the credit of the editors that they adopted a liberal approach to the selection of contributors to this volume, in which this contrast between "island biogeography as metaphor for theoretical ecology" and "islands as real places with complex dynamics" is on display. Even so, there is much about island biogeography as a field of study that is left out. Examination of the index illustrates well what is and is not covered here: among the topics generously represented in the index are the terms *archipelagoes*, *birds*, *colonization*, *competition*, *divergence*, *diversity*, *equilibrium*, *exploitation*, *extinction*, *food web*, *habitat fragmentation*, *immigration*, *metapopulation dynamics*, *neutral theory*, *population biology*, *predators*, *trophic regimes*, and *turnover*. Not appearing in the index, and absent conceptually from many chapters in the volume, are the terms *adaptive radiation*, *geology*, *historical*, *persistence*, *phylogeography*, *phylogenetics*, *reproduction*, *speciation*, *tectonics*, and *vicariance*.

Not all of MacArthur and Wilson's insights continue to bear fruit. It is striking that a field of study that blossomed and became prominent in the 1970s and 1980s as an outgrowth of the 1967 volume, that of life history tactics as typified by the terms *r*- and *K*-*selection*, has seemingly disappeared, supporting the contention of Lomolino et al. that a contraction of the 1967 theory took place. Another, greater contraction is discussed below: the exclusion of speciation as an intrinsic, dynamic process in island biogeography.

The volume begins with a brief retrospective by E. O. Wilson on the origin of the 1963 paper and 1967 book, followed by two insightful chapters that focus on the early development and tests of the equilibrium model, by Lomolino et al. and Schoener; these should be required reading for any student of island biogeography. All three chapters make it clear that the intent of the 1967

volume was to de-emphasize the role of geological change and the long-term historical development of island biotas, and to develop a theoretical framework that was ecological, mathematical, and subject to direct experimentation and testing. It was, in my personal estimation, an effort to model the maintenance, not the origin, of biodiversity, because aside from brief sections that Lomolino et al. point out as having been lost in a subsequent contraction of the theory, it explicitly excluded "deep-time" and evolutionary phenomena.

It is tempting to divide the remaining chapters into two groups, those that fall within the framework of the 1967 volume, and especially that of the iconic equilibrium model, and those that strike out into new territory. That, however, would be badly misleading. Chapters by Hanski, Holt, Hubbell, Laurence, Simberloff & Collins, Terborgh, and Velland & Orrock all deal with issues intrinsic to the equilibrium model and theoretical aspects of ecological dynamics of species at a community level, and in that sense they carry on the tradition. However, those by Hanski and Laurence, and Holt to a substantial extent, explicitly view patterns of species richness and community composition as representing the sum of disparate parts that must be analyzed independently, and they decry an "excessive emphasis on species-area relationships" (Hanski, p. 209), and advocate analysis of single-species incidence functions and the complex and hugely varied differential colonization and extinction patterns, based on species' autecology. The contrast could hardly be more extreme with the perspective of Hubbell, who largely accepts the implication of the equilibrium model that "species [are] ecologically equivalent ... in their probabilities of immigrating ... and going extinct" (p. 264). Hubbell sees the simplicity of the equilibrium model as one of its greatest strengths, and states that we should "... add complexity slowly, ... when absolutely necessary, kicking and screaming the whole time" (p. 288). I believe that, based on chapters in this volume, a strong case could be made that, whether or not there has been kicking and screaming, a new paradigm of community ecology has developed that no longer relies on the equilibrium model as the pri-

mary framework, with great opportunity for new advances that lie beyond its iconic simplifying assumptions.

What, then, has changed since 1967? We can identify, somewhat simplistically, changes that have taken place for two different reasons. First, as shown in many of the chapters, there has been a great deal learned, through application and testing of the equilibrium model and its assumptions. This leads inevitably to recognition that the model is limited and imperfect, perhaps typified by Hanski's statement that "... expectations regarding the MacArthur-Wilson model were too high ... and distracted attention from single-species incidence functions, which would have provided much richer material for research ..." (p. 209), and Holt's comments that MacArthur and Wilson's "... island biogeography continues to provide a powerful metaphor for thinking about habitat fragmentation, ... [but] ... this metaphor can be limited, and at times highly misleading. Habitat fragments in some ways are like islands, but in some ways are radically different" (p. 174). These and other chapters point the way to a new and different paradigm of ecological studies of fragmented populations in island-like ecosystems.

A second change since 1967 took place outside the context of the MacArthur-Wilson theory. In 1967, the concept of plate tectonics was new and hotly debated, but soon came to provide a powerful, widely-accepted model for the evolution of the earth's surface features. With it came evidence of "hot-spots" where plumes of magma give rise to chains of oceanic islands over millions of years. Beginning in the late 1970s, the first intimations of what became molecular phylogenetics appeared, leading eventually to today's robust phylogenies. The islands themselves can have their origins and histories dated with increasing precision, and the phylogenies can be temporally calibrated, though the degree of precision is admittedly currently contentious. All of this allows direct investigation of the processes of speciation in ways that were undreamed of in 1967, and it is the process and impact of diversification that is the basis for the second and perhaps more revolutionary of the changes in perspective.

A number of the authors pointed out that it is somewhat ironic that the 1967 volume made so little of the role of speciation in island faunas, given the prominence of islands in the development of the theory of natural selection and Wilson's research on the systematics of ants; indeed, Wilson's earlier paper on taxon cycles relied heavily on phylogenetic diversification as a primary process influencing ants on Pacific islands. In this volume, speciation and diversification processes are highlighted in many of the papers, along a spectrum of conditions. Clegg, Ricklefs, and Grant & Grant show the process of diversification at early stages, demonstrating genetic changes that immediately follow colonization of islands, anagenetic speciation on isolated islands that results in speciation but not in diversification, and the early stages of diversification among closely-related species, respectively. Gillespie & Baldwin and Losos & Parent document the extensive role of diversification as an intrinsic, dynamic element among biotas on remote islands and archipelagoes, and explicitly emphasize the necessity of studying diversity patterns and community composition over large scales of time and space, and they make a strong case that diversification must be considered as a process that is the conceptual equivalent of colonization and extinction in the formation of island biotas. In what makes explicit a substantial paradigm shift, the chapter by Whittaker et al. takes these observations to their necessary conclusion with their recently developed "General Dynamic Model" of oceanic island biogeography. They present this as an extension of the MacArthur & Wilson 1967 model, but their model is so different from the equilibrium model in its assumptions, components, and predictions that it leads biogeographers to ask an entirely different set of questions from those that naturally emerge from the equilibrium model. Rather than setting aside speciation, the new model places diversification in a central role; and rather than treating islands as static entities, oceanic islands are presented as having "life histories" that have direct, measurable, and predictable impacts on every aspect of the dynamics of island biogeography. Deep history and evolution have been re-incorporated into island biogeography.

It is exciting to see such dynamic development of new approaches to island biogeography; whether one studies metapopulation dynamics, conservation biogeography, or adaptive radiations on oceanic islands, the field of island biogeography continues to offer broad horizons. If it is true that the paradigm initiated by MacArthur and Wilson is being supplanted in both ecological and evolutionary island biogeography, the new paradigms owe much of their development to the robust research agenda laid out 40 years ago.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton.

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Edited by Markus Eichhorn and Joaquín Hortal

book review

Past environmental change in Latin America

Late Cretaceous and Cenozoic History of Latin America Vegetation and Terrestrial Environments, by Alan Graham

Missouri Botanical Garden Press, *Flora Mesoamericana* Vol. 4(1), June 2010, 617 pp. ISBN: 978-1-930723-68-9

Price: \$95.00 (Hardback)

<http://www.mbgpress.info/>

This authoritative text by Prof. Alan Graham of the Missouri Botanic Gardens is based upon nearly four decades of research in the Neotropics. The volume provides a comprehensive foundation for understanding the past environmental change that underlies the biogeographic patterns found in Latin America (defined as 32°N to 55°S), and is a companion volume to his earlier work which focused upon North America (Graham, 1999), in addition to another recent book on the palaeoecological history of the New World (Graham, 2010¹). The introductory note to the Latin America book states that the target level is advanced undergraduate and graduate students, and that the aim is to be appropriate for use within university courses and seminars. In my opinion this book achieves this goal by providing up-to-date information in a well organised, concise and interesting manner.

The book is logically set out and written in an easily-digestible style which should be understood by most undergraduate students. Divided into three sections (Background, Database and Synthesis) and eight chapters, there is a natural progression in the format, which means that the text could easily be utilised as a support for a seminar series or lecture course. The background section contains a wealth of basic information on the climate, geography, geology and vegetation, which provides the scene-setting details which would be required for any undergraduate lecture series on the past environments of Latin America. The clear and consistent geographic organisation of chapters and subsections also lends itself to the teacher or student who wishes to extract information on a particular region of interest; Mexico, the Antilles, Central America or South America.

¹A review of this book will appear in a future issue of *Frontiers of Biogeography*.