

Preface

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ROBERT MACARTHUR AND EDWARD WILSON'S 1967 book, *The Theory of Island Biogeography*, is the dominant symbol of a transition that took place four decades ago from descriptive to analytical approaches in ecology and biogeography. Change was in the air during the dynamic decade of the 1960s, and, both together and independently, MacArthur and Wilson made seminal contributions to ecology and evolution. Had they not written *The Theory of Island Biogeography*, MacArthur and Wilson would still be recognized as two of the most influential figures of this period.

Every contemporary student is taught MacArthur and Wilson's graph with the crossed colonization and extinction curves, along with the astonishing implication that island biotas assume a dynamic steady state in which species continually disappear from islands only to be replaced at an equal rate by new colonists. Few of these students realize that *The Theory of Island Biogeography* also was a compelling call for a comprehensive re-fashioning of biogeographical thinking. Inescapably, biogeography theory fully integrates much of ecology, population biology, evolution, and paleontology, with important implications for conservation of species. Islands and archipelagoes are, in many respects, microcosms of the rest of the world.

The symposium held at Harvard University during the fortieth anniversary year of *The Theory of Island Biogeography* gave both of us an excuse to read this wonderful book (yet again!) and to reflect, as many of the authors in this volume have done, on its legacy. Two aspects of the book stood out for us. First, so much of what we take for granted about the modern disciplines of ecology, evolution, and conservation biology can be traced directly back to one or several of the seven chapters. For example, the relationship between species number and area, the subject of chapters 2 and 3, and certainly one of the dominant empirical patterns in all of biology, has been fully assimilated into theory relating loss of species to habitat destruction, underlies much of spatial ecology, and is a foundational observation for neutral theory. Topics discussed in "The Strategy of Colonization" (chapter 4) are fundamental to present-day areas as diverse as life-history evolution and population viability analysis. Chapter 5, "Invasibility and the Variable Niche," presented a general theory of community assembly and introduced the concept of ecological saturation. "Stepping Stones and Biotic Interchange" (chapter 6) has metamorphosed

into metapopulation biology and landscape ecology. "Evolutionary Changes Following Colonization" (chapter 7) presaged much contemporary research on the success of invasive species.

Second, in contrast, some of the areas emphasized by MacArthur and Wilson remain relatively unexplored or their promise unfulfilled. As the authors pointed out in their first chapter, "the fundamental processes, namely dispersal, invasion, competition, adaptation, and extinction, are among the most difficult in biology to study and understand." This remains true today. By their nature, the processes underlying biogeographic distributions and evolution within the geographic context occur on vast scales of time and space, at least relative to individual human experience. By way of contrast, most tests of equilibrium theory have depended on observations on small islands close to sources of colonists over relatively short periods. The evolutionary dimension is largely missing; the study of haphazard events over long distances has only recently gained ascendancy—partly as vicariant explanations for biogeographic patterns have lost their luster—and the promise of understanding the emergence of biotas *de novo* in remote archipelagoes has yet to be realized. In particular, Ed Wilson's call for the "biogeography of the species" to take a central place in understanding pattern and process in the natural world is just beginning to receive the attention it deserves.

As this volume is published in 2009, the bicentennial of the birth of Charles Darwin, we are reminded of the crucial influence of islands on this most observant and thoughtful of biogeographers. We also are reminded that much of the momentum of Darwin's original insights concerning the origin, distribution, and evolution of species had been lost by the middle of the last century. MacArthur and Wilson's *The Theory of Island Biogeography* was arguably one of the pivotal points in restoring Darwinian traditions of careful observation and reflection to ecology and evolutionary biology, and conveying the excitement of its study. It was the nature of the time, to be sure, but *The Theory of Island Biogeography* made the single most persuasive case for integrating population and evolutionary thinking into biogeographic analysis and interpretation.

This book, and the symposium upon which it was based, sprang from a casual lunch-time realization early in 2007 that the year marked the fortieth anniversary of the publication of MacArthur and Wilson's opus. Encouraged by Harvard's Center for the Environment and Museum of Comparative Zoology, we invited sixteen scholars to participate, including a mixture of older biologists, some of whom began their careers in the buoyant waters pouring forth from *The Theory of Island Biogeography* and the exciting change it represented, and younger investigators who continue to feel the influence of that work. To our amazement, fifteen accepted our offer. All but one symposium participant have contributed chapters, and one additional contributor has been added.

The participants and approximately three hundred symposium attendees endured an unseasonably warm October, 2007, weekend in the un-air-conditioned Geological Lecture Hall at Harvard. They were enchanted by Ed Wilson, who joined us to celebrate the occasion. In his talk, he recounted the origins of the partnership between himself and Robert MacArthur, who died in 1972, and regaled us with stories about the early days of experimental biogeography. We were also pleased that Lord May of Oxford (formerly just Bob to many of us) was available to address the symposium and write a perceptive foreword to this book. We were also gratified that so many of the packed audience were graduate students and postdocs, some of whom came from great distances and, hopefully, left inspired.

The sixteen contributions in this book are loosely grouped into three sections: the history of island biogeography theory, ecology, and evolution. In the first section, Wilson recounts the early days from personal experience, Lomolino, Brown, and Sax review the development of biogeography theory more generally and outline areas of future synthesis, Schoener examines the famous equilibrium model and some of its early tests, while Whittaker, Triantis, and Ladle expand the theory by incorporating the life stages of islands themselves.

Islands, of course, are ecological systems, and many ecological systems have island attributes. These themes are explored with respect to trophic cascades on islands of different size (Terborgh), food web ecology (Holt), metapopulation dynamics (Hanski), conservation in a fragmented world (Laurance), equilibrium theory and assembly rules for island biotas (Simberloff and Collins), and the neutral theory of metacommunity diversity (Hubbell).

Finally, since Darwin's time, islands have provided laboratories for the study of evolution, including changes following colonization (Clegg), species formation (Grant and Grant), the special circumstances of remote archipelagoes (Gillespie and Baldwin), Lesser Antillean birds as a case study (Ricklefs), the role of speciation in building diversity on large islands (Losos and Parent), and the parallels between island biogeography theory and population genetics theory (Vellend and Orrock).

In reading these articles and reviewing the literature on island biogeography, we were struck by two observations. First, the legacy of *The Theory of Island Biogeography* is alive and thriving. When we first envisioned this book, we expected most contributions to be retrospective, reviewing the ideas laid forth in that book and assessing how they had fared. By contrast, a glance at this book will indicate that many of the chapters are looking primarily forward, rather than backward. Some of the most exciting areas in ecology and evolutionary biology—metapopulation theory, the neutral theory of biological diversity, trophic cascade theory, the synthesis of ecological and phylogenetic evolutionary approaches, to name a few—were inspired by or are being integrated with island biogeography.

Much of this work was at most only hinted at by MacArthur and Wilson, yet exciting developments today have a clear intellectual thread leading back to that work, as many articles attest.

Conversely, the field seems to have passed by some of the issues that were at the heart of debate concerning island biogeographic theory in the 1970s and 1980s. As Schoener's article indicates, even though the equilibrium theory was central to the excitement and controversy surrounding the book, its status is currently uncertain. In part, this reflects studies that suggest that the domain of circumstances to which the theory applies is more limited than originally suggested. More generally, though, it simply reflects the fact that few researchers today are measuring rates of colonization, extinction, and species turnover. The crossing-lines diagram may be the most enduring icon of MacArthur and Wilson's book, but work devoted to quantifying such curves and assessing their significance no longer appears to be a high priority.

Similarly, the field of conservation biology was founded when island biogeographic thinking was applied to questions of nature reserve design. The ensuing bitter debate over SLOSS (single large or several small protected areas) played itself out through journal pages and led to the design of many experiments, the most large scale being the "Biological Dynamics of Forest Fragments" project still ongoing in Amazonian Brazil. But, as Laurance's chapter indicates, the field here, too, has moved on, not because the debate has been settled definitively, but because researchers recognize that other issues are more directly relevant in shaping conservation policy.

Books such as this—and the symposia on which they are sometimes based—represent the combined efforts of many people behind the scenes. The symposium held at Harvard University was underwritten by the Harvard University Center for the Environment and the Museum of Comparative Zoology. We thank the directors of these institutions—Dan Schrag and James Hanken—for their support, and Jim Clem, Jenny MacGregor, and Lisa Matthews of HUCE for their tireless efforts to organize and pull off the event. In turn, the quality of this volume was immeasurably improved by the review process. All manuscripts were reviewed by at least two colleagues; in most cases, one was a book contributor and the other an outside reviewer. In addition to the efforts of the contributors, we thank A. Badyaev, J. Chase, B. Emerson, R. Ewers, J. Foufopoulos, N. Gotelli, L. Harmon, L. Heaney, I. Lovette, M. McPeck, T. Price, and D. Spiller. This book could not have been produced without the help of Princeton University Press. Many thanks to J. Chan, K. Cioffi, A. Kalett, R. Kirk, and J. Slater.