doi:10.1111/j.1558-5646.2010.01104.x

THE THEORY OF ISLAND BIOGEOGRAPHY AT AGE 40

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Received July 27, 2010
Accepted July 27, 2010

Review of: Losos, J. B. and R. E. Ricklefs (eds.). 2010. *The Theory of Island Biogeography Revisited*. Princeton University Press, Princeton, NJ. 476 Pages. ISBN: 978-1-4008-3192-0. $99.50 hb; $49.50 pb.

Despite representing only about 3% of the earth's surface, islands have had an inordinately important impact on ecological and evolutionary thinking, beginning with the insights of Darwin and Wallace. Islands and their biotas have long fascinated biologists because of their discrete boundaries and isolation, their limited and disharmonic species richness (compared with mainland biotas), and their spectacular examples of adaptive radiation. Sewall Wright (1940) used islands as metaphors in the early days of population genetics, and island-based books written by Carlquist, Lack, and Mayr strongly influenced ecological and evolutionary thinking in the mid-20th century. But, the seminal event that seemingly revolutionized our thinking about evolution on and the biogeography of islands was the 1967 publication of "The Theory of Island Biogeography" (TTIB) by Robert H. MacArthur and Edward O. Wilson, who were both in their late 30s at the time. This 200-page monograph became an instant classic and has inspired several generations of ecologists, evolutionary biologists, and conservation biologists to add "island thinking" to their conceptual toolkits and research and management programs.

The current volume is based on a 40-year retrospective on the impact of TTIB on ecology and evolution. Authors of the book's 16 chapters span several academic generations and include one of the original authors, Ed Wilson; first-generation intellectual offspring of MacArthur and Wilson (Holt, Hubbell, Ricklefs, Schoener, Simberloff, Terborgh); other older island aficionados (the Grants, Whittaker); as well as younger island researchers (Clegg, Gillespie, Hanski, Lomolino, Losos, Velland). Although TTIB had a strong impact on conservation thinking in the 1970s and 1980s, chapters with an explicit emphasis on conservation are missing from this book ("conservation" has no entry in the index), whose primary focus, as in the original monograph, is on ecology and evolution. This is unfortunate because some of the world's most pressing current conservation concerns come from islands where many plants and animals have suffered accelerated extinction rates via the hand of man.

Although TTIB covered many topics whose interconnections were highlighted in the book's Table 1, the dominant conceptual idea that captured biologists' immediate attention, that has appeared in innumerable ecology texts and lecture notes, and that has inspired myriads of research projects, is the famous "crossed curves" graphs that appear in Chapter 3. These graphs, which encapsulate the "Equilibrium Theory of Island Biogeography" (ETIB), postulate that the number of species living on an island is determined by two primary factors: the rate (C) at which new species colonize an island (a decreasing function of an island's species richness, S) and the rate (E) at which island species go extinct (an increasing function of S). Given that these two rate curves cross, an equilibrium number of species ($\hat{S}$) is inevitable, just as there is an equilibrium size ($\hat{N}$) for a population whose birth and death rates are decreasing and increasing functions of

N, respectively. An important corollary of ETIB is that $\hat{S}$ is a dynamic equilibrium; that is, island biotas experience a constant turnover of species at a rate determined by the crossing point of the two curves. Sometimes viewed as a revolutionary insight, this dynamism is also an inevitable consequence of the crossed input and output curves just as populations that are regulated in density-dependent fashion change constantly in composition while maintaining a stable N. As reviewed by Schoener in the current volume, considerable research attention has been applied to this aspect of ETIB. Unfortunately, most of this work has been done on relatively small spatial and temporal scales that have little relevance to long-term evolutionary aspects of ETIB. Finally, in addition to rates of colonization and extinction, MacArthur and Wilson identified island area and degree of isolation, as indicated by distance from the nearest mainland source of colonists (and, oddly, not a function of the nearest island in an archipelago), as important factors determining an island's $\hat{S}$, which will generally increase with area and decrease with isolation. Island age, which we now know can have a profound effect on S as discussed in chapters by Whittaker et al. and Gillespie and Baldwin, was not included in their theory. Based on recent research, the existence of an $\hat{S}$ for an island is now very much in question.

As MacArthur and Wilson anticipated, much has happened in the research fields of island biogeography specifically and evolution generally in the 40 years since the publication of TTIB, and virtually all chapters reflect this. Some chapters are explicitly retrospective and focus closely on how well various concepts and predictions of TTIB and closely related topics such as Wilson's taxon cycle and Diamond's community assembly ideas have fared under close scientific scrutiny. Others deal with topics that were only lightly touched upon or not mentioned at all in TTIB, including the evolution of body size in island mammals, the effects of generalist herbivores on island plant taxonomic and biochemical diversity, and food web structure on islands. Regarding food webs and community structure, competition and predation continue to dominate island thinking, and interactions such as mutualism and parasitism that can strongly affect species richness and interaction diversity continue to be neglected. These topics deserve a more prominent place in general models of island species richness.

Like TTIB, a majority of the book's chapters have an ecological rather than an evolutionary focus, and Losos and Parent state (p. 416) "that for more than three decades after the book's publication, little attention was paid to evolutionary issues as research focused on the ecological factors affecting species richness." Those chapters with a strong evolutionary emphasis highlight how this is changing and how studies based on phylogenetics and molecular genetics are revolutionizing our view of island biology. For example, in the 1960s it was commonly thought that colonization of islands from mainland sources was unidirectional, but we now know that this is not true. Based on phylogenetic studies, we know that a variety of different organisms, including *Anolis* lizards and several groups of bats originating in the West Indies, have successfully colonized and radiated on the neotropical mainland (reviewed in Bellemain and Ricklefs 2008). Molecular phylogenetic studies have also shown that single colonizing lineages are often the sources of adaptive radiations of plants, insects, and birds on isolated oceanic archipelagoes and that in situ speciation has contributed significantly to the total number of species living on an island. Over 90% of the 100 or more species of *Anolis* lizards on large islands in the West Indies are products of intra-island speciation. A similar situation occurs in *Bulimulus* snails in the Galapagos. These and other studies indicate that large islands, even those that are not strongly isolated from the mainland, are not constantly being colonized and that endemic taxa often contribute significantly to their species richness. Other molecular studies, for example, of the pteropodid bat fauna of the Philippines, have shown that species can persist on islands for long periods of time, even on small islands (Heaney and Roberts 2009). Extinction and species turnover are thus not inevitable in some (many?) island taxa (but see Ricklefs' chapter for a dramatic example of apparent extinction in the birds of the Lesser Antilles).

Molecular studies are also refining our understanding of the genetic consequences of founder events associated with island colonization. As reviewed by Clegg, avian colonizations can sometimes result in some loss of allelic diversity, but heterozygosity seldom declines during the early stages of colonization. A decade or so ago it was believed that island populations generally contain less genetic diversity than mainland populations, but recent studies of island birds and bats do not always support this generalization (see Clegg and chapters in Fleming and Racey 2009). Small populations of island birds and bats often contain substantial amounts of genetic diversity and exhibit little propensity to suffer from inbreeding depression. Their main extinction risks come from anthropogenic forces, not genetic forces.

The relative importance of allopatric versus sympatric speciation has been strongly debated in recent decades, and island studies have contributed to this debate. The Grants review the evidence for sympatric speciation in *Neospiza* buntings in the Tristan da Cunha islands and in *Geospiza* finches in the Galapagos and conclude that this evidence is currently equivocal. Speciation in both systems is more likely to have been allopatric than sympatric. Similarly, Losos and Parent conclude that allopatric (in different habitats) or microallopatric (in different parts of the same habitat) speciation has generated the large number of endemic species of *Anolis* that exist on the large islands of the Greater Antilles.

Perhaps the most prominent recent use of TTIB as inspiration for general theory is Hubbell's "Unified Neutral Theory of Biodiversity and Biogeography," published in 2001. As in TTIB, Hubbell treats species in communities of competitors as being demographically equivalent regarding birth (=colonization in TTIB) and death rates (=extinction)—that is, species are ecologically neutral—and assumes that species' distributions are dispersal limited. In his chapter, Hubbell uses simulation models to demonstrate that ecological equivalence can evolve in species under most (but not all) reasonable conditions regarding resource and species' distributions. Despite the fact that neutral theory can predict the relative abundances of tree species on the 50-ha Barro Colorado plot; however, Hubbell concludes (p. 288) that species' identities and ecological characteristics do matter and that a full understanding of tropical forest dynamics will come from ". . . a non-neutral, niche-based theory of ecology from the perspective of statistical mechanics." It is likely that MacArthur and Wilson would have reached a similar conclusion regarding the importance of species' identities and ecological characteristics if they had continued to pursue TTIB post-1967.

In the end, like the *Origin of Species*, TTIB must be viewed in an historical context. Both of these seminal and highly cited works were pioneering attempts to explain how evolution and ecology operate in the world and on islands, respectively. Neither could or should have been expected to provide a definitive treatment of these topics. The fields of evolutionary biology in general, and island biogeography specifically, are much richer in theory and empirical data now than when these inspirational works were published. Many of the major advances in "island thinking" are reviewed in detail in the chapters of Losos and Ricklefs. For this reason, this book is a worthy successor to TTIB, and its chapters are well worth reading and discussing by evolutionary biologists and ecologists.

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Book Review Editor: J. Thompson