The Theory of Island Biogeography Revisited

Author: Currie, David J.

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novel model involving *APETALA2* was proposed but not explained in enough detail for me to completely grasp it. For this reason, I think the book may be most useful for the thousands of scientists coming from the molecular genetic side of the evolutionary development (evo-devo) divide. The many botanical tidbits and morphological oddities are certain to open the eyes of biologists whose experience with plants begins and ends with *Arabidopsis* and perhaps rice or maize. For those from the botanical and evolutionary side of evo-devo, *The Molecular Organography of Plants* represents a useful starting place and will help point them in the right direction with its extensive references. I can certainly recommend it for both types of scientists, particularly at the graduate level.

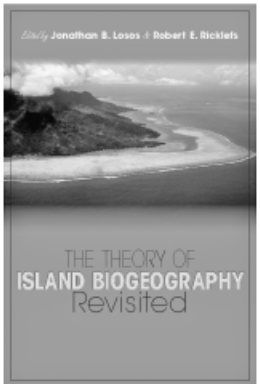
ELENA M. KRAMER
Elena M. Kramer (ekramer@oeb.harvard.edu) is a professor of Organismic and Evolutionary Biology at Harvard University in Cambridge, Massachusetts.

THE GLASS HALF FULL

The Theory of Island Biogeography Revisited. Jonathan B. Losos and Robert E. Ricklefs, eds. Princeton University Press, 2009. 494 pp., illus. $49.50 (ISBN 9780691136530 paper).

The Theory of Island Biogeography Revisited is the fruit of a symposium held at Harvard in 2007 in honor of the 40th anniversary of the publication of Robert MacArthur and E. O. Wilson's *The Theory of Island Biogeography (TTIB)*. The organizers of the symposium invited a who's who of community and island ecologists. Sixteen participants produced chapters for the book; the result is a very good overview of a wide body of work that draws inspiration from, but does not necessarily directly follow, *TTIB*. The text of this new work is accessible, readable, and often engaging. I was motivated to read it cover to cover, and even to buy another copy after I misplaced my first one. I have suggested the book to my new graduate students as a font of interesting ideas for their research proposals.

The Theory of Island Biogeography Revisited could easily serve as the centerpiece of a graduate course, in part because of its very discussable shortcomings. The book begins with reviews of how island biogeography theory came to be (recounted by Wilson), then discusses subsequent tests of the theory (reviewed by Schoener and Lomolino and colleagues). Neither chapter explicitly states any conclusions, but Schoener's indicates that the bulk of the evidence is consistent with



TTIB (the glass being fairly full). Laurence discusses fragmentation effects in nature, commenting that although *TTIB* may be a conceptual Mount Everest, it is "simplistic to the point of being cartoonish" (the glass having obvious emptiness).

A second portion of the book (which is not explicitly organized in thematic sections) focuses on work that was inspired by ideas in *TTIB*. Notable among these is metacommunity theory. Hanski discusses metapopulation models beginning with *TTIB* and Levins's work from the same era, continuing through his own work. Chapters by Holt and by Terborgh examine trophic relationships on islands, going beyond *TTIB*'s emphasis on species counting. A third part deals with community assembly. Simberloff and Collins review the notions of assembly rules and checkerboard distributions in a chapter redolent of the late 1970s (except for want of a companion chapter by Diamond). Hubbell contrasts predictions from neutral theory and from Tilman's R* theory, testing them against his Barro Colorado Island data (there is no matching piece from Tilman).

The lion's share of *The Theory of Island Biogeography Revisited* is devoted to reviews of evolutionary effects on islands. Several chapters pertain to the dynamics of colonization, speciation, and hybridization—illustrated by the birds of the Galápagos (by the Grants, framed as an homage to "Ed Wilson the Naturalist"), birds of the Lesser Antilles (Ricklefs), as well as anoles of the Antilles and snails of the Galápagos (Losos and Parent)—or discuss islands more generally (Clegg, and Gillespie and Baldwin).

Although the chapters were generally quite good, I was disappointed by the book. First, there are no abstracts. Abstracts force authors to identify their central message. The book would have been more interesting and more useful if the authors had been expected to make an identifiable conceptual advance in their chapters. Second, in a book with this title, I thought I would see tests of and successors to *TTIB*. A classic MacArthur quote is: "To do science is to search for repeated patterns, not simply to accumulate facts" (from the preface to his *Geographical Ecology*). *TTIB* presented general patterns and then proposed a mechanism that made explicit predictions about the observed patterns (variation of richness with area and with isolation) and how the patterns should look under new circumstances (e.g., during habitat fragmentation or during initial colonization of an island). The resulting statistical models accounted for quite a lot of the geographic variation in species richness. Therefore, I expected to see assessments of the limitations of *TTIB* (e.g., that *TTIB*'s scope is limited to particular archipelagos), and modified models that

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address those limitations (e.g., D. H. Wright's 1983 species-energy work). I thought I might see meta-analyses comparing the conditions where *TTIB* failed empirical tests with conditions where it passed, followed by more general models that address those limitations and failures.

However, this book contains strikingly little systematic examination of general patterns. Rather, there were often lists of processes that can affect species distributions (e.g., niche preemption, founder effects, sympatric speciation, etc.), followed by a supporting example or two (i.e., some accumulated facts). Evidence was very often presented to support, rather than test, ideas. In particular, given the emphasis on evolutionary processes, there was surprisingly little effort to statistically incorporate these into modifications of *TTIB*, or to assess to what extent variation in biotic assemblages among islands can be statistically related to differences in evolutionary processes, versus differences in contemporary environment. Only one chapter of this book seems to start explicitly with *TTIB* and further develop its concepts: Whittaker and colleagues extend *TTIB* to include island age as a factor influencing island richness.

My third reservation is philosophical. Vellend and Orrock, in the concluding chapter of the book, put their finger on it. Comparing the fields of community ecology and population genetics, they remark that community ecology developed in light of obvious patterns in nature (e.g., latitudinal variation in richness), whereas population genetics developed as a theoretical discipline in the absence of much data on allele frequencies. Thus, Vellend and Orrock say, "although population genetics appears to rest on a firmer theoretical foundation than community ecology, we are not actually any better at predicting broad scale patterns of genetic diversity than we are at predicting broad scale patterns in communities. If anything, the opposite is true." But—and here's the rub—"the difference is that in population genetics this is not considered a short-coming given the coherent set of basic models that can be successfully tailored to meet the inherently contingent specifics of any particular case, whereas in ecology we are set up for disappointment when we hope for grand all-encompassing theories to make the contingencies disappear" (p. 453). Vellend and Orrock then propose an organizational structure for community ecology on the basis of population genetics.

This argument gets to the question of what science is supposed to do. On the one hand, if the purpose of science is to develop theories that predict the behavior of nature, then one may ask: What can we predict now, 40 years after *TTIB*, that we could not predict in its immediate wake? Dismayingly little, judging from this book. On the other hand, one may argue (as Vellend and Orrock seem to say, and plenty of other chapters in this book seem to do) that the purpose of science is to elucidate mechanisms that operate under at least some circumstances (e.g., in controlled experiments), and to provide a plausible example or two from nature to illustrate those mechanisms. Thus armed, one can sally forth to explain (a posteriori) the contingent specifics of particular cases. In this view, this revisitation of *TTIB* will be very satisfying. Even for die-hard predictionists (such as myself), *The Theory of Island Biogeography Revisited* has a wealth of ideas whose general predictive ability begs testing.

DAVID J. CURRIE
David J. Currie (dcurrie@uottawa.ca) is a professor in the Biology Department at the University of Ottawa, Canada. He is editor in chief of Global Ecology and Biogeography: A Journal of Macroecology, *published by Wiley-Blackwell.*

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