The Important Role of Theory in Conservation Biology

The Unified Neutral Theory of Biodiversity and Biogeography. Hubbell, S. B. 2001. Princeton University Press, Princeton, New Jersey. 448 pp. $29.95 (paperback). ISBN 0-691-02128-7.

Bangham and Asquith (2001) note that biologists have, for many years, been good at measuring things, and that what mathematical theory contributes to biology is not quantification but a "precise qualitative framework of reasoning." This volume falls squarely into the valuable tradition of providing models to help us sharpen our thinking. It has already been reviewed in *Science* (de Mazancourt 2001), *Nature* (Abrams 2001), and *Evolution* (Brown 2001) and described as "on its way to becoming a classic in the biodiversity and species abundance literature," "big, ambitious, creative, important," and containing "many interesting ideas and intriguing new findings." Here, I will discuss matters not covered in those reviews (themselves worth reading) and will focus on conservation biology.

Hubbell sets out with three goals: to explore the implications of a formal, neutral theory for biodiversity; to show how the mechanisms in the formal theory are important to the assembly and dynamics of ecological communities; and to demonstrate the predictive power of this neutral theory. The book is in many ways the true successor to MacArthur and Wilson's *The Theory of Island Biogeography*, which gave conservation biology two key tools: (1) a qualitative theory for the number of species on an island being determined by the balance of colonization and extinction rates and (2) a quantitative tool for predicting the stochastic dynamics of population size for a single species. Hubbell gives us a powerful new tool that allows the simultaneous evaluation of the number of species in a community and the number of individuals of each species.

Hubbell's neutral theory assumes that all individuals are ecologically equivalent in terms of per capita rates of birth, death, migration, and speciation. He calls this ecological drift and identifies it as demographic stochasticity. His inclusion of speciation as a per-capita rate is a lynchpin of the theory because it allows the prediction of both number of individuals and number of species. In the theory of MacArthur and Wilson, neutrality is defined at the species level—for example, the balance of colonization and extinction rates as functions of the number of species already present. In Hubbell's theory, neutrality occurs at the individual level. Neutral theory is profound because it assumes that communities are collections of species whose biogeographic ranges overlap for historical and stochastic reasons rather than because of tight coadaptation.

A community consists of J individuals, with the number of individuals proportional to area (A), $J = \rho A$. A key assumption is that J is approximately constant; Hubbell refers to this as the "general principle that large landscapes are essentially always biotically saturated with individuals." The number of individuals within a species fluctuates according to a birth and death process (simplest case) modified by migration and speciation (more complicated cases). In the birth and death process, the probabilities of an increase of one individual or a decrease of one individual within a given species are the same; this is the neutrality assumption in action. The deterministic version of these models is a series of uncoupled logistic-like differential equations with a globally stable equilibrium.

The key parameter that emerges in the analysis is the "fundamental biodiversity number," $\theta = 2Jv$, where v is the speciation rate. In general, the size of the community J is very large and the speciation rate is very small, so their product is of an intermediate value. The parameter θ determines both the equilibrium species richness and the relative species abundance in the community, and this parameter is asymptotically (for the number of individuals in the community going to infinity) equal to Fisher's α. Hubbell shows, in fact, that his models are the same as the log series that Fisher used, in the limit of infinite population size. We thus have a way to understand Fisher (usually a task in itself) and have a version of the log series for finite numbers of individuals. Furthermore, the asymptotic equivalence shows that if data fit the log series of Fisher, then they are consistent with the neutral theory. Together, the parameters of community size, migration, and fundamental biodiversity determine all properties of the community. Important results jump out at one. For example, the theory predicts that on islands common species will be commoner and rarer species rarer than in the source metacommunity. Another simple (and obvious, once it is presented) result concerns rarefaction curves. Begin with the standard species-area relationship $S = cA^z$, and then rewrite the constant as $c = c'\rho^z$; we get $S = c'J^z$, so the number of species in a sample increases as a

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power (<1) of the number of individuals in the sample. Similarly, the neutral theory explains patterns in the exponent z of the species-area relationship (Rosenzweig 1995) in terms of the dispersal parameter at different spatial scales.

Throughout the book, Hubbell shows the fit of the neutral model to various sets of data, and he provides a chapter on generality and testing the theory. He offers no discussion, however, on deviations between the theory and data. What do such deviations mean? Are they the result of observation error or process uncertainties not included in the model? (For instance, in many cases populations can change by more than one individual in a very short period of time.) There is no formal competition, for example, between the neutral theory and other theories; such competitions would be the most convincing evidence of the value of the neutral theory.

A review should always pick some nits. I am disappointed that Hubbell makes made no mention of the wonderful work of Edward Fager (1957, 1968) in which communities are viewed as recurrent groups of organisms. This idea is similar in spirit to Hubbell's. He is a bit cavalier with mathematical notation, and this quibble is more than just pedantry. For example, his initial formulation (p. 49) of the equations characterizing population change are (strictly) mathematically incorrect, although he offers a caveat about them (for the correct formulation see Mangel and Tier 1993). Students trying to use these could be mislead, frustrated, or confused. Similar problems occur elsewhere in the book, because the level of mathematical presentation is uneven. In his detailed explanation of transition probabilities for birth and death processes, Hubbell assumes that readers know what the infinitesimal mean and variance of a diffusion process are in his summary of work by Engen and Lande (p. 72), and he assumes a sophisticated knowledge of linear algebra and matrix manipulation. At times the notation is lumbering (e.g., F_2^{t+1}) and the equations are not numbered, making it difficult to refer back and forth to them. One of Hubbell's emerging principles is that "biodiversity is intrinsically fractal," but—other than sounding cool—it contributes little to our understanding of biodiversity or conservation.

Has Hubbell achieved his goals? Yes, most definitely. This is a valuable book. Buy it; look through it; study it. Every encounter with the book will give you something new to think about.

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Literature Cited

Abrams, P. 2001. A world without competition. Nature **412**:858–859.

Bangham, C. R. M., and B. Asquith. 2001. Viral immunlogy from math. Science **291**:992.

Brown, J. H. 2001. Toward a general theory of biodiversity. Evolution **55**:2137–2138.

de Mazancourt, C. 2001. Consequences of community drift. Science **293**:1772.

Fager, E. W. 1957. Determination and analysis of recurrent groups. Ecology **38**:586–595.

Fager, E. W. 1968. The community of invertebrates in decaying oak wood. Journal of Animal Ecology **37**:121–142.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Mangel, M., and C. Tier. 1993. Dynamics of metapopulations with demographic stochasticity and environmental catastrophes. Theoretical Population Biology **44**: 1–31.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, New York.

Neotropical Mammalogy by Popular Demand

Mammals of the Neotropics. 3. The Central Neotropics: Ecuador, Peru, Bolivia, Brazil. Eisenberg, J. F., and K. H. Redford. 1999. University of Chicago Press, Chicago. 609 pp. $80.00 (hardcover). ISBN 0-226-19541-4. $40.00 (paperback). ISBN 0-226-19542-2.

This book was published, according to its authors and editors, in response to popular demand. After the success of two previous volumes that dealt with the so-called "Northern Neotropics" (Panama, Colombia, Venezuela, Guyana, Suriname, and French Guyana) and with the "Southern Cone" (Chile, Argentina, Uruguay, and Paraguay), many were interested in a book focusing on the South American region not covered in the preceding books. This new volume concentrates on the "Central Neotropics"—Brazil, Ecuador, Perú, and Bolivia—an enormous and still cursorily known area. It comprises, for instance, most of the Amazon region; large parts of the Andes; the Cerrado, Caatinga, and Atlantic forest regions in Brazil; and part of South America's Pacific coast (including a special reference to the Galapagos and other islands, on both the Atlantic and Pacific Oceans). These are diverse areas, still covered mostly by natural vegetation (with the exception of the Brazilian Atlantic region and a few other areas, which are highly threatened).

The authors' purpose was to capture the state of the knowledge of mammals in this remarkable region at the end of the twentieth century. The structure of the book is similar to that of the previous volumes. An introductory chapter is followed by sections on biogeographic and historical issues, taxonomic accounts, and mammalian community ecology. The introductory chapter briefly describes the study region and the history of mammal collecting in the area. The second section of the book, with contributions by David Webb, Alceu Rancy, and Castor Cartelle, reviews Plio-Pleistocene South American mammalian faunas, emphasizing the western Amazon and the Cerrado and Caatinga ecosystems of eastern Brazil, placing them in an evolutionary and ecogeographic time frame. Prominent topics in these chapters are the succession of faunas, the evolution in