

Deep-Sea Biodiversity: Pattern and Scale

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detailed description of molecular signaling between rhizobia and legumes is engaging because Douglas clarifies the implications of such findings for understanding symbioses in general, discussing this work in the context of “partner choice” and “conflict management.” I would suspect that people more familiar with specific intimate symbioses would likewise find stimulating her discussion of examples of less intimately associated organisms and their relevance to general principles of symbiosis.

Indeed, this is the strength of the book: Through Douglas’s narrative, researchers interested in molecular-level interactions and signaling between organisms find common ground with ecosystem scientists. The fact that these examples are interwoven and not separated in discrete sections is key, making it impossible for even “skimmers” to miss the parallels. One such parallel lies in Douglas’s discussion of symbioses as an interacting community of symbiont species or genotypes within a single host (whether it’s multiple microbes in the gut of a vertebrate or organelles within a eukaryotic cell), rather than the pairwise interactions between a single host and symbiont. This mirrors recent studies of mutualisms among macroorganisms that move beyond pairwise mutualisms to multiple ant or fungal associates of a single host plant or even mutualistic networks among many host plants and their overlapping pollinators. In this discussion, Douglas makes predictions about the outcome of interactions involving multiple symbionts on the basis of the extent to which symbionts provide distinct versus overlapping benefits to the host, pulling examples from both intimate symbioses and loose associations among free-living organisms.

Overall, *The Symbiotic Habit* provides a detailed yet readable overview of many conceptual issues surrounding symbiosis, and the range of examples also illustrate the importance of the topic to most biologists. Although Douglas provides plenty of examples and rich detail, she wisely

avoids attempting to write a comprehensive volume, rendering the book fewer than 200 pages of text and readable from cover to cover.

Douglas writes in her closing chapter that the breadth of symbioses studied gives strength to symbiosis as a discipline; she clearly demonstrates this with the phylogenetic and habitat diversity of the book’s examples. In her words, symbiosis is “not simply a type of interaction in the continuum of benefit and harm. It is a first-order process in the evolutionary diversification of living organisms, a crucial element to physiological function of most eukaryotes, and a major determinant of the structure of ecological communities.” In *The Symbiotic Habit*, the reader will find an authoritative glimpse into the fascinating world of symbiosis and the concepts that are emerging from recent advances.

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MEASURING UP THE DEEP

Deep-sea Biodiversity: Pattern and Scale. Michael A. Rex and Ron J. Etter. Harvard University Press, 2010. 368 pp., illus. \$55.00 (ISBN 9780674036079 cloth).

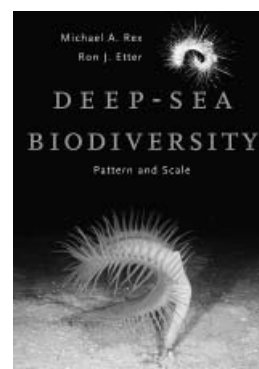
No scientist could challenge the assertion that Earth is the most biodiverse planet in the solar system. Few would challenge that lower-latitude ecosystems are more biodiverse than higher-latitude ones. But in this game of “biodiversity trumps” there are some closer calls. In the early 1990s, Fred Grassle and others challenged the ecological community with an assertion that the deep sea—cold, dark, and still fairly poorly sampled—could rival or exceed tropical rainforests and coral reefs for biodiversity. It was an

astounding claim, and although the authors were careful to qualify it, they were widely criticized for the daring of their extrapolations. Nevertheless, high deep-sea diversity is now an established paradigm, and the excellent new book *Deep-sea Biodiversity: Pattern and Scale*, by Michael A. Rex and Ron J. Etter, provides a veritable barrage of data-missiles to hurl at any terrestrial-based doubters.

Those scientific missiles are not hurled by these authors, however. Indeed, this is a calm, analytical, and elegantly written book that leads the reader neatly through the most important studies in deep-sea ecology. It may feel like a book in the hand, but it reads like a polished review paper; the prose is wonderfully clear and concise. There are no flights of fancy, complex analogies, or firsthand accounts of derring-do on the high seas. There is just the data, the analyses, and the ideas of two highly respected researchers in the field.

The book, as befits its subtitle, is organized around the concepts of pattern and scale. It starts with a review of quantitative data on abundance and food supply, building then through chapters on local diversity, regional diversity, beta diversity, and finally the evolutionary origins of deep-sea biodiversity. Processes are invoked throughout, and the final chapter aims—and partially succeeds—at a challenging synthesis.

The chapters that discuss broader, macroecological trends in deep-sea biodiversity are the highlights; they build on several papers by the authors themselves



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and present a thorough review of how biodiversity patterns shift across two of the planet's greatest physical gradients—depth and latitude. *Deep-sea Biodiversity* presents the most convincing case yet for the unimodal pattern of species richness with depth, and provides an excellent discussion of the relative roles of actual ecological processes versus the bias of the mid-domain effect. With regard to the gradient in diversity with latitude, criticism has arisen of the authors' own papers on this subject. To their great credit, however, this section presents a comprehensive review of both sides of the argument, with the admission that low diversity in Norwegian Sea samples heavily (but not completely) influenced the patterns they published in their 1993 paper in *Nature*.

There has been a resurgence of interest in reproduction and dispersal as processes influencing deep-sea diversity patterns. Dispersal is probably a key process driving deep-sea biodiversity from both ecological and evolutionary points of view. One idea that relates dispersal to the bathymetric gradient in diversity is the source-sink hypothesis, first promoted by Rex and coauthors in a 2005 paper in *American Naturalist*. The premise is simple: The food-impoverished abyssal fauna are not reproductively viable, and these small populations are sourced from reproductive propagules that have come from larger populations at bathyal depths—hence the lower abyssal diversity. As with the authors' 1993 latitudinal-gradient paper, the source-sink idea has been criticized for its application only to mollusks from a limited range of samples. Deep-sea biologists (myself included), in discussions and in print, have since been keen to point out various samples containing healthy-looking abyssal species, their stomachs packed with food and their gonads packed with eggs. But, to be fair, Rex and colleagues have always been at pains to emphasize that their hypothesis was specifically to explain molluscan patterns, and they reiterate this here, making little play of source-sink dynamics as a “general theory” in deep-sea biology.

The concept of dispersal reappears in the final chapter on evolution. Here,

the authors present what I believe to be one of the main paradoxes in deep-sea biology: If deep-sea species have such powers of dispersal, and if the habitat boundaries are so unconstrained, then how can so much speciation have taken place? There are perhaps two answers. The first is that deep-sea species are not all that good at dispersing across the vast distances of the abyssal plains. Here, Rex and Etter point out that many so-called cosmopolitan species may in fact be “constellations of cryptic species”—a wonderful turn of phrase that reflects the haplotype maps that geneticists use to illustrate them. Molecular genetics is now confirming this for some groups of species, but not all. The second idea, explored extensively in this final chapter, is that changes in depth are the most powerful boundaries to dispersal. I would argue that the deep sea is not characterized by its deepness as much as by its huge range of different depths. In this concept, the bathyal regions are the engines of speciation, fueled by cyclic changes in paleo-oceanographic processes.

Howard Sanders and Robert Hessler published the first comprehensive, quantitative studies on deep-sea biodiversity in the late 1960s. Rex and Etter's book is dedicated to them and is a worthy tribute. Sanders and Hessler would (and will) no doubt be pleased that their ideas have withstood another 40 years of quantitative sampling, and that there is still enormous interest in the undoubted mystery of the deep sea.

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DO WE NEED GEOENGINEERS OF THE EARTH SYSTEM?

Linkages of Sustainability. Thomas E. Graedel and Ester van der Voet, eds. MIT Press, 2009. 430 pp., illus. \$40.00 (ISBN 9780262013581 cloth).

L*inkages of Sustainability*, an edited volume of 25 chapters, intends to document and synthesize the research of nearly 50 contributors, mostly from developed countries, who have attempted to better frame the multiple dimensions of global Earth system sustainability. Known for its interest in basic theoretical research in fields such as biology, the Ernst Strüngmann Forum of the Frankfurt Institute for Advanced Studies outlined the theme for this volume in 2006, and the forum's steering committee identified Thomas Graedel and Ester van der Voet (industrial ecologists and editors of this book) as focal participants. Other participants from various disciplines were then invited to Frankfurt for a weeklong meeting in 2008. A deliberate focus of this meeting was to more fully understand, from the angle of complex systems sustainability, the specific linkages among energy, water resources, nonrenewable resources (i.e., minerals), and renewable land resources (e.g., forests, croplands, ecosystem services, institutions, human and social capital).

Following an introduction by Graedel and Van der Voet (chapter 1), several background chapters offer the essence of “group discussion” for each of the book's four areas—land, minerals, water, and energy—with a summary chapter concluding each grouping. The editorial tandem ends the book with remarks on the emergent importance of better investigating potentially sustainable linkages among these resources. The brief introduction in chapter 1 defines the book's language and specifies the use of related middle-range models such as substance (or material) flow analysis, input-output analysis, trade-off evaluation, and life-cycle assessment (e.g., stocks, flows, rates). The background chapters of each resource area range in style from the data-rich but atheoretical overviews (chapters 2, 7, 23) to the theory-driven critical reflections on methods, concepts, or research strategies (chapters 3, 14, 21) to model-driven research articles

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