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In a World of Diversity, a Search for Unity

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Abstract. Holyoak, Marcel, Mathew A. Leibold, and Robert D. Holt, editors. 2005. **Metacommunities: spatial dynamics and ecological communities**. The University of Chicago Press, Chicago, Illinois. xi + 513 p. \$95.00 (cloth), ISBN: 0-226-35063-0 (alk. paper); \$38.00 (paper), ISBN: 0-226-35064-9 (alk. paper).

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Understanding the dynamics of multispecies communities has traditionally been the purview of community ecology and food web theory. But in those fields the emphasis is largely on the processes that govern the stability, composition, and relative abundance of species within a single community with little consideration of interactions between communities. The developing field of metacommunity ecology attempts to fill the gaps in our understanding of the influence of intercommunity interactions. The view of metacommunity ecologists is that the organization and dynamics of species communities arise from the reciprocal influence of local and regional processes. According to this view, to understand the properties of a given community one must consider not only the environmental conditions and species interactions that occur locally but also the processes that connect the community to other communities near and far. This book attempts to articulate this multi-scale perspective by synthesizing the concepts and models developed within the fields of community ecology, metapopulation biology, island biogeography, and food web theory. Synthesis is a journey whose end is unification. What metacommunity theory seeks to unify is our understanding of the mechanisms and processes that determine species persistence, coexistence, and spatial distribution in communities.

This book reviews the theoretical heritage of metacommunity ecology, summarizes the current state of the field, and proposes a framework for tackling the difficult task of unification. It is a collaborative effort initiated during a symposium on metacommunities held at the 2001 annual meeting of the Ecological Society of America and later continued by the Metacommunity Working Group at the

National Center for Ecological Analysis and Synthesis. In addition to the three editors, 30 people contributed to the volume. The topics range from modeling and theory to the results of empirical studies. The intended audience includes graduate students and researchers in theoretical and applied ecology.

The book is organized into 20 chapters arranged in four sections that address conventional themes. The introductory chapters are devoted to explaining key terms, describing essential concepts, and explicating the metacommunity viewpoint. The “Core concepts” chapters describe foundational issues such as the opposing influence of species sorting and mass effects. The book reviews spatially implicit and explicit two-species models, consumer-resource interactions in multi-species, multi-trophic food webs, and the relevant literature. Much of the information presented here is not new and can be found elsewhere. But students and researchers will be delighted to find material of such breadth organized and summarized in a single volume. Topics addressed in the “Empirical perspectives” section include an interesting discussion of the multitrophic interactions of butterfly metacommunities, the influence of local and regional processes on pitcher plant communities, two experimental studies that focus on the effects of habitat fragmentation (one on invertebrate communities that inhabit bryophytes, the other on beetle metacommunities in a eucalyptus-pine mosaic), and two chapters that examine the effect of environmental heterogeneity on zooplankton species patterns (one using shallow ponds in Belgium, the other using small rock pools in Jamaica). While the chapters in this section are intended to highlight recent empirical results, they just as importantly contribute interesting hypotheses that both complement and broaden the concepts discussed in other sections of the book. The empirical chapters, while a bit of a hodge-podge, reveal that central themes are beginning to emerge that give shape to the metacommunity perspective. For example, it is a natural choice for examining the effects of habitat fragmentation on species diversity.

Early on, the book attempts to show that metacommunity ecology is a logical extension of the fields of community ecology, metapopulation biology, etc. This view is reinforced by the many tables, charts, and discussions presented throughout the book that draw connections across the literature and trace the theoretical development of each field. This deliberate attempt to find common ground imparts thematic cohesiveness and direction to the book, strengthening its message. It also enhances the book's pedagogical value and usefulness as a reference. However, ecologists disagree on what constitutes the principal structuring forces of community organization, and any attempt at synthesis must address this dissent. The editors do recognize this disparity, which they describe as competing frameworks that emphasize different mechanisms for community patterns. These are identified as the patch-dynamic perspective, the species-sorting perspective, the mass effects perspective, and the neutral perspective. But while the editors explain the differences among the perspectives, they stop short of suggesting how they might be reconciled toward the goal of synthesis. The incongruity of the four competing hypotheses remains the biggest obstacle to building a comprehensive theory of metacommunity dynamics. Given the collaborative nature of the work here, I was surprised that it omits a plan for tackling this central problem. Some aspects of the problem are taken up later in the book (e.g., Chapter 10), but I was disappointed that the editors chose to blithely side-step the issue.

Chapters 10–19 wrestle with other theoretical and conceptual issues that remain tough challenges for unification. Topics include an excellent review and assessment of source-sink dynamics and competition-colonization trade-offs, and a graph-based model of assembly dynamics that addresses the multi-scale nature of metacommunities. Two chapters (12 and 13) are devoted to scale transition theory which attempts to formalize the relationship between local nonlinear dynamics and spatial averaging which becomes important at regional scales. Here, species coexistence at the metacommunity scale is governed by the interaction between spatial variance and covariance in species densities across communities with local scale interactions and population dynamics within communities. The upshot is that spatial variation can disrupt the mean-field community patterns that would arise by simple averaging in the absence of spatial heterogeneity. The chapter on scale transition theory is one of the

highlights of the book. I found it to be an exceptionally well-written and accessible presentation of this important topic.

At 513 pages, the book is hefty than similar review-and-synthesize books. I found the construction of the paperback volume to be solid. The pages are off-white, smooth but not glossy. I noted a few errors (e.g., it is clear from the caption that Figure 2.1 is turned 90 degrees from its correct orientation). The material is clearly presented and the quality of writing is generally high. In its liberal use of tables and diagrams, the book serves as an excellent introduction to the foundational concepts and theoretical lineage of metacommunity theory. It certainly is an excellent choice for a graduate seminar, although it would be difficult to cover in its entirety, given the duration of a single semester.

This work is not the first attempt to unify ecology under the banner of spatial scale and process. But five years ago Stephen Hubbell created quite a stir with his ambitiously titled monograph *The unified neutral theory of biodiversity and biogeography* (2001. Princeton University Press, Princeton, New Jersey). Hubbell's singular focus on the explanatory power of neutral dynamics made his theory the target of much criticism. It's a good bet that the present volume will also have its critics. The difference here is that the contributors do not introduce a new theory so much as co-opt several different research areas into a single topic. Metapopulation biology, community ecology, food web theory, and island biogeography often reach different conclusions about which processes impart structure to species communities. The overarching view expressed in this book is that understanding multi-scale, multi-species spatial dynamics is the key to reconciling these different perspectives. Without a recognizable plan, this sanguine outlook seems to overlook the enormity of the undertaking. Some ecologists may therefore be skeptical of the notion that such disparate models and theories can be neatly subsumed under the banner of metacommunity ecology. Controversy may ensue, but controversy is generally good for progress in science. This book is certain to stimulate discussion about whether and how ecologists ought to go about searching for a unified theory.