Conservation beyond Community

Metacommunities. Spatial Dynamics and Ecological Communities. Holyoak, M., M. A. Leibold, and R. D. Holt. 2005. 524 (513 + xi) pp. $38.00 (paperback). ISBN 0-226-35064-9.

Years ago, when I first heard the word *metacommunity*, I resisted it. The basic idea was that community ecology needed a regional perspective. Space, after all, was ecology's last frontier (Kareiva 1994). But my gut reaction was to avoid the new "meta" expression. Did we really need a new term to add to the already rich metapopulation language? What would the concept contribute above and beyond traditional community ecology? Was it all just metaphysics envy? Since that time, my appreciation for the metacommunity concept has grown in reaction to an expanding and compelling body of theoretical and empirical work on the subject. The previously diffused and disconnected metacommunity research has now been synthesized into one book, *Metacommunities: Spatial Dynamics and Ecological Communities*, which provides a synthesis of past research, clarifies a nascent lexicon, and proposes new extensions and frontiers. Metacommunity ideas are still largely theoretical and as yet can deliver few practical conservation predictions. However, the metacommunity concept has substantial promise to spur a spatially integrated and more accurate perspective for conserving diversity in fragmented landscapes. In this respect, the book

presents a compelling case for adding the metacommunity concept to the ecological toolbox. I suggest that you add it to your bookshelf.

Metacommunities explores what happens when community ecology operates within an interconnected mosaic of habitat patches. In contrast to the more familiar metapopulation approach, local interspecific interactions determine each population's local extirpation risk. Hence, the metacommunity framework elevates community processes to a dominant role in determining local persistence. This assumption adds a layer of complexity to spatial ecology heretofore largely neglected. *Metacommunities* will engage community ecologists looking to broaden their erstwhile, limited spatial scope and metapopulation ecologists who cannot escape from the knotty complications that arise when multiple species interact. The hope is that the two will meet on amicable terms—an optimistic expectation by any measure. But through inclusiveness and sheer breadth, editors Marcel Holyoak, Mathew Leibold, and Robert Holt manage to unify these camps into a compelling framework. For the conservation biologist, many of the ideas are still early in their development and provide little in the way of hard and fast solutions. Practical applications await feedback from ongoing empirical assessments. That said, the metacommunity approach offers a useful theoretical construct that includes the biological realities of complex multispecies interactions over multiple spatial scales. This integrated perspective hints at the promise of improved future conservation recommendations.

Metacommunities is divided into four parts. The first describes the assumptions and core concepts of metacommunity theory. These chapters introduce a prevailing focus of the book: comparing and contrasting four divergent ideas about metacommunity assembly. These ideas are termed the patch-dynamics, neutral, mass-effects, and species-sorting perspectives. Each perspective differs in its assumptions about the strength of spatial coupling among communities, the magnitude of environmental heterogeneity, and the effect of heterogeneity on species fitnesses. Together, these concepts provide a steady progression from community dynamics determined largely by dispersal to those that relegate dispersal to correcting the match between species traits and local conditions. That metacommunity variation can be explained along an organizational axis of interpatch migration and environmental heterogeneity suggests a compelling hypothesis—one of many to originate from the metacommunity vantage point. However, as noted in later chapters, these templates are not mutually exclusive and not all species in a region or even a local community can be expected to adhere to the assumptions underlying a single perspective.

The second section presents empirical examples detailing how local species interactions and dispersal jointly affect local and regional community patterns. The take-home message is that changes in communities cannot be predicted without understanding the role dispersal plays in counteracting local extirpation. Although empirical examples are compelling, the reader should not expect a polished understanding of real-life metacommunities. The rarity of empirical work on metacommunities renders synthetic conclusions impossible. Instead, book examples function as a feedback on emerging theory by highlighting current inadequacies. Of profound and apparently general relevance is the problem that each species can disperse over widely divergent scales. Yet most theory assumes equivalent dispersal rates among species. This result limits the applicability of current theory and highlights the chasm that must be crossed before conservation biologists are likely to use metacommunity models.

Both synthesized and novel theories on metacommunities are merged into the last two sections. The reviews of mass effects (a form of sink source dynamics for multiple species), competition colonization tradeoffs (Mouquet, Hoopes, & Amarasekare), and spatial-storage effects (Chesson, Donahue, Melbourne, & Sears) are impressive and accomplished with rare clarity. Anyone requiring a refresher or an introduction to these complex concepts will benefit from these chapters. Additional chapters break new ground. Although not as accessible as review chapters, new models of multispecies community assembly in space (Law & Leibold), neutral communities (Gomulkiewicz & McPeek), and the metaecosystem (Loreau, Mouquet, & Holt) are presented. This last concept proposes an integration of metacommunity and landscape ecology such that flows of energy and materials across boundaries inform predictions of community diversity and emergent ecosystem properties such as biomass production. A chapter by Resetarits and others illustrates how incorporating the behavior of habitat selection into a regional perspective leads to a more complex, yet realistic, portrayal of species movement. This spate of theoretical work offers a variety of novel ideas that will continue to push the theoretical envelope while we wait for empirical research to catch up.

The final chapters reveal an emergent theme of the book—that strong similarities exist between metacommunity and genetic theories of coexistence and diversity. The analogous changes that occur as genetic and species diversity are sorted among divergent environments provide both a call for integration and a bountiful pool of population genetic theories to adapt for ecological use. The retooling of neutral genetics for neutral metacommunity theory illustrates this latter approach. Here, McPeek and Gomulkiewicz argue that macroevolution often builds species so similar in form that they have comparable fitnesses. Therefore neutral metacommunity perspectives

co-opted from the genetic literature often may prove useful. In this same thread, Leibold, Holt, and Holyoak highlight similarities between evolution by natural selection and metacommunity dynamics. This chapter suggests that a more comprehensive view of biological diversity can be focused through the integrated lens of complex adaptive systems (Levin 1998).

The book ends with an assurance of more to come for the application minded. In this regard, readers hoping for a deeper examination of conservation implications may feel disappointed. However, the metacommunity approach does offer some general insights. One conservation outcome that materializes from metacommunity research is a "Goldilocks" principle for the effect of dispersal on species diversity. Dispersal that is too low precludes the ability of immigrants to rescue local populations declining due to unstable interspecific interactions. Dispersal that is too high synchronizes patch dynamics and precludes the possibility of rescue effects. Hence, the highest local diversity is predicted at moderate (just right) dispersal rates that counteract local extirpation threats and, depending on assumptions about patch heterogeneity, realign species with optimal habitats following patch disturbance or succession. But this outcome depends critically on the strength of local interactions and variation in dispersal rates. Hence, metacommunity theories make strong cases for understanding dispersal rates of threatened species and for applying adaptive management strategies that account for interconnections between remnant patches within the larger regional landscape. The hope remains that more robust, applied predictions will be forthcoming.

Overall, *Metacommunities* should be recognized as a substantial and successful synthesis of existing theoretical and empirical work. The book integrates a bevy of competing ideas into a coherent and expanding metacommunity ecology field. In the process, the reader will be convinced of both its possibilities and liabilities. Perhaps this is what I like most about the book: its editors and writers freely admit and accept the challenges provoked by a metacommunity view. I believe that one of the thorniest challenges for the concept is that it remains faithfully tethered to the strong interactions that tie it to traditional community ecology. In the absence of species interactions, the metacommunity reduces to a more tractable metapopulation of multiple species. Herein lies my strongest criticism of the book. I had hoped it would provide stronger guidance on the strength of interactions necessary to justify a metacommunity approach. The problem is that enterprising researchers may apply the metacommunity term to suggest a novelty where one does not exist. This threatens to muddy ecology's metaterminological waters. A corrective measure would place the weight of evidence on researchers to demonstrate the primacy of interspecific interactions in the local extirpation process.

My personal standard for a book is that it changes how I think about a subject. This book met this criterion. *Metacommunities* makes an excellent case that metacommunity theory is not just metapopulation theory for the 00s. Substantially different dynamics from those predicted in metapopulation models result when dispersal enmeshes the local dynamics of multiple interacting species. I believe the book will encourage readers to understand how regional linkages affect local ecological outcomes in their own systems. In the process, I expect that the metacommunity framework will increase the future rigor and accuracy of conservation biology.

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