



## Large-scale Perspectives in Community Ecology

Community ecology has reached an impasse in recent years. Many ecologists have been frustrated by the inability of often arduous, small-scale experiments to result in generalizations that can be accurately applied to other communities over larger time scales. Compounding this, the enormous number of components within communities has forced many model-based and computer-savvy ecologists to develop increasingly cumbersome mathematical models. Although it is true that these developments are slowly advancing the ability of ecology to untangle the myriad species interactions within ecological communities, there are still significant hurdles that must be crossed in order to develop successful general principles of community structure, and many feel that time is running out on endangered communities. Guided by this growing frustration of small-scale ecological experiments in recent years, community ecologists have been undergoing a dramatic change in perspective with the advent of an approach named macroecology [1, 2].

Providing an important update of this emerging field, Maurer's latest book argues that a more comprehensive and holistic understanding of ecological processes can be grasped when researchers turn away from the reductionistic, experimental approach at small temporal and geographic scales and turn toward significantly larger scales, analyzing multispecies assemblages over tens to thousands of years and over continental to global geographic ranges. Maurer cogently argues that the reason microecological studies are limited in their explanatory power is that they sample only a minuscule portion of much larger, complex natural systems. When one steps back from this perspective and views the system more holistically, the noise inherent within small subsets gives way to the emergent patterns of the

system as a whole, which are often ergodic and stable at larger scales.

Maurer's book is in some ways a companion to James Brown's classic, *Macroecology* [2]. In fact, Maurer makes frequent reference to many of the large-scale interspecific ecological patterns illustrated in Brown's book, ranging from relationships between range size and abundance, range size and body mass, and population density and body size, and it is worth having this text available as a visual aid because Maurer generally does not reproduce the figures. However, Maurer goes one step further by developing quantitative models based on population dynamics and geographic range sizes of species to test whether specific ecological mechanisms are responsible for the observed patterns. Several of his more successful models are derived from Lotka's classic equations and used to model the population densities of interacting species within communities over time or to model the geographic range of a species based on its demographic dynamics. This tying together of demographic processes, including dispersal, immigration, and extinction, to the geographic range of a species is Maurer's greatest accomplishment in this text and offers a novel and promising approach to community analysis. Maurer develops this geographic range model further to test its ability to accurately represent three patterns often found within continent-wide interspecific assemblages (the species-area curve, the distribution-abundance relationship, and the pattern of nestedness), and I briefly chronicle them here to illustrate the benefits of macroecological approaches.

The species-area relationship builds on the observation that there are typically limits to the number of taxonomically related or ecologically similar species (i.e., insects, birds, mammals) that can co-exist within any given geographic area. When geographic areas of varying sizes are com-



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pared, there is generally a positive, log-linear relationship between the size of the sampled area and the number of species sampled within each region. In a similar vein, when the abundance (or population density) of many related species are plotted against the number of samples in which that species was present, there is generally a positive, linear relationship. This distribution-abundance relationship essentially shows that common (or "core") species have wide geographic distributions, whereas rare (or "satellite") species have restricted distributions. Finally, there is a nested relationship among communities of different sizes, so that low species richness communities are typically composed of the more common species in other, more diverse communities. Interestingly, these patterns are found within many taxonomically and ecologically unrelated groups; however, the mechanisms responsible for the patterns are far less well known.

These patterns were originally discovered by ecologists attempting to understand why some species appeared in some communities, but not in others. Assuming that all species within the local species pool potentially shared an equal chance of inhabiting a particular habitat, ecologists traditionally explained this variability by appealing to the unique attributes of individual species or to the interactions (including predation, competition, and mutualism) among individu-



als within the community. Although these small-scale hypotheses have had some empirical support in explaining community structure, Maurer provides an alternative mechanism that relies on the higher level properties inherent to a species total geographic range. In this scenario, he posits a causal relationship between the total geographic range of species and the taxonomic composition of individual sites within that region, without directly implying biotic interactions or habitat preferences in the community structure. This model assumes that each species has a Gaussian abundance distribution (an assumption that is empirically valid to a first approximation) and, therefore, that a species does not have equal access to all geographic sites within a specific region. From these assumptions he shows that a species will have a greater probability of occurring at greater abundance at the more centrally located sites within its geographic range. Given the different geographic ranges of different species within a region, local communities should be composed of different species exhibiting different population densities, with the most widespread species simultaneously present at the most sites and at the greatest population densities within those sites. When compared with other models based on the characteristics of individuals within the community, Maurer's model, termed geographic range analysis, better approximates the empirical large-scale community patterns described above.

Maurer's model, however, does not exclude small-scale influences. In fact, it is precisely these influences, including genes and their effects on phenotypes and the consequent ecological characteristics of individuals, that pro-

duce the geographic range of each species. (However, Maurer does not adequately explain how these lower-level characteristics result in different population-level growth, dispersal, extinction, and immigration rates). But rather than build his ecological model based on these lower-level characteristics, Maurer treats geographic range as an emergent species-level property in order to develop more predictive larger-scale theories of community composition. Ultimately, Maurer contends that these higher-order characteristics also determine the propensities of species to speciate and to go extinct on geologic time scales.

Throughout the book, Maurer makes clear that he does not expect that macroecology will replace more traditional experimental ecological approaches that focus on smaller-scale factors, such as competitive interactions, predation, or population dynamics. In fact, he argues that the results of such studies should be used to test the predictions of larger-scale generalizations in order to develop more comprehensive hypotheses. Such an approach circumvents the necessity of intractable large-scale experiments, focuses on using previously collected data in novel ways, and is generally applicable with less time or money. Maurer is right in noting that this nonmanipulative approach is much more similar to that of cosmology than to the experimental sciences; unfortunately, he neglects to mention that just such an approach has been common in paleobiology for decades (e.g., Ref. 3). Part of this legacy in paleontology stems from the historic need for the government and petroleum industries to have an accurate biostratigraphy with which to define geologic strata.

The result has been a rich record of fossil communities that for years awaited compilation by paleobiologists into computer databases for future analyses and that has fueled many large-scale research programs [4, 5]. Furthermore, macroecology would benefit from a closer relationship with paleobiologists, as the time-averaging inherent to most fossil assemblages essentially removes the small-scale noise that obscures the recognition of macroecologic patterns while maintaining a good approximation of preserved species abundance over temporal scales from tens to thousands of years [6, 7].

As science has so often proven, fresh discoveries from examining old problems are frequently linked to new perspectives. With its large-scale and interdisciplinary perspective, let us hope that the suggestions and techniques offered in this book for testing patterns in nature are heeded by all those scientists interested in community ecology, whether of living or fossil assemblages.

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#### REFERENCES

1. Brown, J. H.; Maurer, B. A. *Science* 1989, 243, 1145.
2. Brown, J. H. *Macroecology*; University of Chicago Press: Chicago, 1995.
3. Sepkoski, J. J., Jr. *Milwaukee Public Museum Contributions in Biology and Geology* 1982, 51.
4. Benton, M. J. *Numerical Palaeobiology*; In Harper, D. A. T. (ed.), Wiley: Chichester, 1999, p 249.
5. Miller, A. I. *Paleobiology*. 2000, Supplement 26, 53.
6. Kidwell, S. M.; Flessa, K. W. *Annu. Rev. Earth Planet. Sci.* 1996, 24, 433.
7. Olszewski, T. *Paleobiology* 1999, 25, 226.