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Book review

Untangling Ecology?

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A review of Brian A. Maurer, *Untangling Ecological Complexity: The Macroscopic Perspective*, University of Chicago Press, Chicago, IL, 1999, 252 pp, ISBN 0-226-51133-2, $18.00.

Untangling Ecological Complexity (UEC) presents Maurer's version of an auspicious research program dubbed "macroecology" by Brown and Maurer (1989). In his own book on the subject *Macroecology* (1995), Brown defined it as

> a nonexperimental, statistical investigation of the relationships between the dynamics and interactions of species populations that have typically been studied on small scales by ecologists and the processes of speciation, extinction, and expansion and contraction of ranges that have been investigated on much larger scales by biogeographers, paleontologists, and macroevolutionists. (pp. 6–7)

"Typical" community ecology, then, traces the effects of local species interactions such as predation, mutualism, and competition. According to Maurer, "mesoecology" examines processes at a somewhat larger spatiotemporal scale: migration, colonisation, and extinction. And macroecology operates at a larger scale yet: the "*geographic scale* . . . on which entire geographic ranges of species exist" (p. 5). Despite the common subject matter, UEC differs significantly from *Macroecology* in style and emphasis. UEC is the more theoretical of the two. In *Macroecology*, Brown remarked that "There is much scope for rigorous mathematical modeling to strengthen the conceptual basis of macroecology" (p. 7). Maurer's book can be seen as an effort to do just that.

Before elaborating his own theory, Maurer presents a critique of traditional community ecology, which he faults for producing too few robust generalisations. The integrated discussion of scale and generality sets UEC apart from most philosophical discussions of general laws in ecology or biology as a whole. UEC has more in common on this score with fellow ecologist Lawton (1999), who is also pessimistic about finding general laws in community ecology, but optimistic about discovering them at the "macroscale".

I found UEC most valuable for its characterisation of Lotka-Volterra community matrix analysis – part of its critique of community ecology – rather than for its exposition of macroecology. As a philosopher with active research interests in community and geographical ecology, I found the book often intriguing, but less frequently convincing or compelling. In this review, I will focus on the issue of general laws in ecological science.

Maurer spends the first two chapters of his book laying conceptual groundwork. In Chapter 1, "Of Entangled Banks and Humble Bees," he asserts that "Laws are the consequence of the interaction of a tremendous number of small particles . . ." (p. 7). According to this view, science can make sense of systems with very small numbers of components, and those with very large numbers, but not "middle-number" systems. However, Maurer never quantifies (even roughly) how many entities are necessary for statistical order to emerge. This omission seriously weakens his oft-repeated claim that local communities do not contain enough "particles":

> The reason that uniqueness rather than regularity characterises local communities is twofold. First, even though there may be many species (especially when decomposer trophic levels are considered as part of the community), there are not enough of them to ensure that each contributes only a very small effect on community patterns . . . Second, community boundaries are relatively permeable to effects from outside those boundaries. (Chapter 3, pp. 56–57)

The last sentence in the above quote reinforces a gloss that also appears in Chapter 1, of traditional community ecology as a failed attempt to treat local communities as approximately closed systems.

Chapter 2, "From Micro to Macro and Back Again", lays out Maurer's views on statistical thinking and the hierarchical structure of ecological systems. Like other conceptual reformers in biology, Maurer tries to ground his ideas in thermodynamics. Chapter 2 also submits a central premise of macroecology:

> if we hope to discover regularities or generalities in ecological systems, we must seek them at appropriately large spatial and temporal scales. If we do not, then we will end up looking at the unpredictable, nonrepeating

> dynamics of individual systems that fail to capture the true nature of the processes we study. (p. 35)

Chapters 3 through 5 present Maurer's critique of small-scale community ecology. Chapter 3 addresses the experimental component of this research program; Chapters 4 and 5, different aspects of its theoretical component. The lynchpin of Maurer's case against the relevance of small-scale experiments is a study showing that the effects of many experimental perturbations decay over time. After just a few years, the communities treated in this meta-analysis reverted back to their original states, despite whatever changes had been experimentally induced. Maurer attributes this reversion to "larger-scale effects infused into the experimental system from its ecological context" (p. 60). Fair enough. However, in the case of the one experiment that he treats in detail, the "larger-scale" effect was still very much local, and involved interspecific competition, a process that he himself places in the purview of traditional, small-scale community ecology.

This example deals with the response of ants to the experimental removal of rodents, with whom the ants compete for seeds, in the Chihuahuan Desert. "[F]or the first two years of the experiment, densities of ant colonies were about twice as high on rodent removal plots as on control plots", due to competitive release.

> However, by the third year, ant colonies were nearly equally dense on both control and experimental plots. Second, from the fourth year on, ant colony densities declined, nearing extinction by the eleventh year of censuses. (UEC pp. 60–61)

The reason had to do with competition, not between the ants and rodents, but between the different seed-bearing plant species.

> Rodents eat larger seeds than ants. These large-seeded plants compete with the smaller-seeded plants preferred by the ants. Any initial advantages to ants that occurred in response to rodent removal were lost when the large-seeded annual plants began to out-compete smaller-seeded annuals. (p. 61)

The competitive suppression of small-seeded by large-seeded plants thus took longer than the ants' initial numerical response to rodent removal. In other words, the former occurred at a larger temporal scale than the latter. However, neither the temporal nor the spatial scale of plant competition reached even the "mesoscale", let alone the macroecological scale, identified by Maurer himself. Instead, all of the phenomena cited lie firmly in the province of the small-scale community ecology he seeks to discredit.

Maurer's critique of small-scale community theory (as opposed to experimentation) is somewhat more convincing. He defines "linear community theory" as

> that body of ecological and evolutionary theory that uses community matrices and Lotka-Volterra-like descriptions of communities to derive theoretical predictions regarding community structure and dynamics. (pp. 85–86)

Chapter 4 provides an illuminating history and analysis of such theory, starting with the work of Alfred Lotka. Maurer concludes that, like ecological experiments, "community matrix analysis is scale dependent, only adequate to predict over relatively short time scales" (p. 86). One reason is that such analysis only applies when species populations are close to equilibrium. Disturbances of various kinds limit the amount of time that populations spend at or near such equilibria.

Maurer does not emphasise other potential problems with Lotka-Volterra-type (LV) community theory. For example, LV theory is couched in terms of population dynamics, but most communities comprise so many species that it is impossible to track all of their population trajectories. There is thus a gap between what the theory invokes and what field ecologists can possibly measure. In the context of the global extinction crisis, "There is simply not enough time, skilled personnel, and money to make detailed field studies of the population biology of all species before they go extinct" (Brown 1995: 213). Over-reliance on LV, population-dynamics-based community theory may have also led some ecologists to employ faulty definitions of community stability (Mikkelson 1997).

The probabilistic model developed by Holt et al. (1999) represents one kind of departure from LV community theory. Their model characterises communities in terms of the simple presence or absence of different species, without attempting to also specify the changing population size of each and every species. With respect to empirical testing and application of their theory, their approach thus stands a chance of avoiding the practical problem noted above by Brown. The theory developed in UEC departs from LV theory in a different way. Rather than eschewing population analysis, Maurer scales it up from local communities to entire species ranges.

After considering, and rejecting, nonlinear adjustments to linear community theory in Chapter 5, Maurer proceeds to his own program in Chapters 6 through 9. Just as UEC as a whole begins and ends with references to Darwin, this set of chapters begins and ends with evolution. Chapter 6 models the evolution of body size in order to explain observed relationships between body size, population density, and geographic range size.

Chapter 7, "Geographic Range Structure: Niches Written in Space" exhibits a model based on an intriguing analogy between species and gases:

$$\rho a = Nf,$$

where ρ is the "population pressure" generated by the species' tendency to increase beyond environmental limits, a is the area occupied by the species, N is the total number of individuals in the species, and f is the per capita rate at which N is changing. Recall that the ideal gas law is

$$PV = nRT,$$

where P is pressure, V volume, n and R constants, and T temperature. This makes the analogy, as well as certain ways in which it fails, clear. For instance, Maurer suggests that "population pressure ... be interpreted as the average rate of dispersal [e.g., in response to crowding] per unit area" (p. 145), which nicely corresponds to the pressure exerted per unit area by a gas (ρ corresponds to P). a for area just as plainly corresponds to V for volume. However, the analogy between f and T is less straightforward, and while n (the number of gas molecules) is not affected by the other variables in the gas law, the total population size N is affected by the other variables in the species law. What is more, the per capita rate of change in the population, f, must depend on N. To wit, the per capita rate of population increase must decline (at least at some point) as the population grows. Otherwise, the population would expand forever.

After elaborating the above model, Maurer suggests that it might enable ecologists to "predict the size of ... geographic ranges directly from ... demographic characteristics" (p. 150). Whether or not that project succeeds, the model could motivate interesting research, such as measuring "net flow of individuals from central, high-abundance populations to peripheral, low-abundance populations within the geographic range of a species" (due, presumably, to population pressure; p. 157).

Chapter 8, "Geographic Assembly of Local Communities", explores several patterns at the "metacommunity" level – that is, patterns that show up across a set of local communities in the same region. These include species-area relationships, links between distribution and abundance, and nested subsets. Maurer correctly observes that such patterns enable ecologists to do a better job of predicting "which species are more likely to persist at a given site over time, and which are more likely to go extinct" (p. 171) than micro-level minimum-viable-population ("MVP") analyses. But his main point is that of three models that he tested, his "geographic range structure" model best explains the metacommunity patterns in question. By "structure", he means the size, shape, and orientation of, and the distribution of abundance within, a species' geographic range.

However, the two other models, "passive sampling" and "habitat heterogeneity", seem like straw men in this context. They both lack key features that should be built into them. For instance, the passive sampling model assumes that species are equally abundant in the regional "pool" from which they are sampled, rather than building in the well-known fact that species differ greatly in abundance. The habitat heterogeneity model not only assumes equally abundant species, but also leaves out an essential feature of habitat heterogeneity: that different species are adapted to different habitats, and are therefore not equally likely to colonize any of the habitat patches, as Maurer assumes. Thus, his results do not support the claim that geographic range structure is an important cause of the metacommunity patterns in question. Rather, they merely indicate the importance of interspecific differences in abundance and/or adaptation. These problems of model construction and interpretation, along with other faults, make 8 the weakest chapter in the book.

Chapter 9 returns to Darwin and evolution – macroevolution, that is. Macroevolution involves speciation, extinction, and major morphological change, while microevolution is change in gene frequencies within populations. Darwin is best known for linking the two. Maurer finds in the *Origin of Species* the roots of another theory, linking macroecological patterns, such as size of geographic ranges and how abundance varies across them, with macroevolutionary patterns of differential speciation and extinction.

Finally, Chapter 10, "The Macroecological Perspective and the Future of Ecology", applies macroecology to the biodiversity crisis. While Brown (1995) offers more specifics in this regard, Maurer does show how a macroecological perspective can offer general insights. Macroecology's focus on the scale of entire species ranges highlights connections between different populations, communities, and ecosystems – and the untoward consequences of breaking those connections.

> An isolated ecosystem must make all energy flow and nutrient cycle 'budget sheets' balance. If it does not, the ecosystem will lose parts (i.e., populations of some species will go extinct). But local ecosystems connected to the biosphere can 'ride out' times when there might be a net energy loss or nutrient deficiency because these will eventually be augmented by flows from connected ecosystems. Many populations may operate in a similar manner.

Such ecological systems "persist by virtue of their connections to larger systems" (p. 209).

In this brief summary and critique of UEC, I have focused on its basic conceptual agenda. I should also point out that the book is quite rich in theoretical and empirical detail, some of which is technically sophisticated. It is beyond my competence to judge the accuracy and relevance of many of these details. Where the book touched on subjects closer to my expertise (e.g., in Chapter 8), I found it unsatisfying.

Nevertheless, UEC pursues a laudable goal: clearing a path for the discovery of robust laws in a science that has driven many authors to pronounce it incapable of yielding any. UEC also hints at an underlying ontology that could potentially guide the search for such laws: hierarchy theory's categorisation of small-, middle-, and large-number systems. However, the book does not specify this ontology to anywhere near the extent necessary to support Maurer's arguments against community ecology, or in favor of macroecology.

It is my sense that general laws will be just as forthcoming at the community level as anywhere else in ecology. For example, even Lawton (1999) held out the hope of finding regularities in food-web structure. Experiments on relationships between biodiversity and ecosystem function suggest other generalisations. Macroecology, then, simply adds one more exciting place to look for laws.

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