ECOLOGY:

How Do Communities Come Together?

A review by Nicholas J. Gotelli*

Ecological Assembly Rules Perspectives, advances, retreats
Evan Weiher and Paul Keddy, Eds.
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Occasionally in the history of science, a pivotal publication changes the direction of a field. For community ecology, one such paper was Jared Diamond's "The assembly of species communities" (1), which summarized over a decade of field research on the avian communities of New Guinea and its satellite islands in the Bismarck Archipelago. Diamond distilled his results into simple "assembly rules" that described broad patterns of species co-occurrence in natural communities. For example, he found that some species of fruit-eating pigeons in the Bismarck Archipelago never co-occurred: an island might harbor species A or species B, but never A and B together. Diamond called this pattern a "checkerboard" distribution and attributed it to competition between species for limited resources.

Such assembly rules have been an important research focus of ecologists ever since, and they are the subject of this symposium volume edited by Evan Weiher and Paul Keddy, which includes 14 diverse contributions. Unfortunately, the editors' introductory chapter obscures rather than illuminates the research. In their rambling essay, they dwell on the sociology and pop psychology of academic controversy instead of carefully framing the scientific issues that led to the assembly rules debate. The essay's profanity, sexual innuendo, and discussion of the merits of human masturbation are bizarre, to say the least, and are an embarrassment to the discipline.

Moreover, Weiher and Keddy present a distorted picture of what constitutes community assembly rules. They claim that two paradigms are developing: a "trait-environment paradigm" in which assembly rules specify the traits of species that allow them to occur in particular habitats, and an "island paradigm." The latter includes the competition-based rules that Diamond proposed, as well as stochastic models of island colonization, which actually provide null hypotheses for testing Diamond's rules.

There is a long-standing tradition in plant ecology of mapping traits onto environments, but this leads to trivial assembly rules. (For example, "The water level in the [prairie] potholes acts as a filter determining the kinds of plant species that will occur there; the two key states are drained vs. flooded.") Diamond's paper would never have generated such controversy or stimulated so much research if simple habitat associations were the basis for assembly rules. The book, however, should not be judged solely on the basis of Weiher and Keddy's introduction. Fortunately, most of the contributors approach the subject with a broader, more analytical perspective, and many of the chapters undercut the editors' claims concerning the topic's domain.

Why did assembly rules become so controversial? In 1979, Edward Connor and Daniel Simberloff published a provocative response to Diamond entitled "The assembly of species communities: chance or competition?" (2). They asked what community structure would look like in the absence of competition. To answer their question, and to provide an operational test for assembly rules, they used computer simulations to generate artificial or "null" communities. These were created by reassigning species to islands randomly and independently of one another. Thus the null communities were formed without the structuring influence of interspecific competition. The surprising result was that many of the patterns predicted by Diamond's rules could also be generated by a null model that, on the face of it, was competition-free.

Similar null models turn up in other areas of biology (3). Population geneticists will recognize the Hardy-Weinberg equilibrium as a null model for expected genotype frequencies in the absence of selection and other evolutionary forces. Similarly, the molecular clock is a null model for the accumulation of neutral genetic variation in an evolving lineage. Null models had been used previously in community ecology, notably by European plant ecologists in the 1920s (4) and by the animal ecologist C. B. Williams in the 1940s (5). But Connor and Simberloff's paper popularized the approach, forcing ecologists to ask how patterns in nature would appear in the absence of a particular mechanism (6). Their aggressive attack on Diamond's ideas also highlighted a growing schism between theoretical ecologists, who emphasized the importance of competition in structuring vertebrate communities, and experimental ecologists, who emphasized the importance of predation, disturbance, and other mechanisms in structuring invertebrate and plant communities.

The controversy in ecology over null models and competition raged through the early 1980s (7). Although the contentious debates have subsided, the controversy is by no means over. For example, three of the papers in this volume debate the significance of a recently proposed assembly rule: interspecific competition leads to "favored states," an even representation of species in different functional guilds (sets of ecologically similar species). Using null models with different underlying assumptions, Barry Fox, Daniel Simberloff *et al.*, and Douglas Kelt and James Brown draw different conclusions as to the importance of the favored states rule in desert rodent communities.

A sensitive issue in the original assembly rules debate was that Diamond's occurrence data for bird species in the Bismarck Archipelago were never published in their entirety, which precluded direct tests of his hypothesis. Attitudes and regulations about data sharing have changed since 1975, so all of the participants in the favored states debate at least are working with the same data sets.

The volume's most worthwhile contribution is by J. Bastow Wilson. He tersely presents a catalog of currently proposed assembly rules and describes the null models that have been used to test them. Drawing on his own studies of the assembly of plant communities, Wilson also discusses how environmental heterogeneity can obscure assembly rules and suggests some creative solutions to that problem. This chapter is the single best overview of the state-of-the-art in community assembly rules.

No major syntheses or breakthroughs emerge from this volume. But it does a good job of illustrating the increasingly sophisticated use of null models to test community patterns. Twenty five years after their publication, Diamond's ideas on assembly rules are still being studied and debated. *Ecological Assembly Rules* highlights many facets of the current research program.

References

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