Review: How Do Communities Come Together?

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Ecological Assembly Rules. Perspectives, Advances, Retreats. by Evan Weiher; Paul Keddy

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BOOKS: ECOLOGY

How Do Communities Come Together?

Nicholas J. Gotelli

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.

Ecological Assembly Rules
Perspectives, advances, retreats
Evan Weiher and Paul Keddy, Eds.
Cambridge University Press, Cambridge, 1999. 430 pp. $90, £55. ISBN 0-521-65235-9.

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 en-

BROWSINGS

The Amber Forest. A Reconstruction of a Vanished World. *George Poinar Jr. and Roberta Poinar.* Princeton University Press, Princeton, NJ, 1999. 247 pp. $29.95, £18.95. ISBN 0-691-02888-5.

The fossilized resin of extinct algarrobo trees provides a rich record of plants, invertebrates, and small vertebrates that inhabited tropical forests on Hispaniola 15 to 45 million years ago. Because many organisms were trapped in mid-action, the amber preserves predator-prey clashes, insect-plant interactions, and parasitic relationships. The image above shows an exodus of Allantonematid nematodes from their Drosophilid host as captured in the amber. The authors have studied Dominican amber for many years, and their photographs and detailed drawings illuminate this fascinating summary of the forest's biota and paleoecology.

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tirety, 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

1. J. M. Diamond, in *Ecology and Evolution of Communities*, M. L. Cody and J. M. Diamond, Eds. (Harvard Univ. Press, Cambridge, MA, 1975), pp. 342–444.
2. E. F. Connor and D. Simberloff, *Ecology* **60**, 1132 (1979).
3. M. H. Nitecki and A. Hoffman, Eds., *Null Models in Biology* (Oxford Univ. Press, Oxford, 1987).
4. O. Järvinen, *J. Biogeogr.* **9**, 363 (1982).
5. C. B. Williams, *Patterns in the Balance of Nature* (Academic Press, New York, 1964).
6. N. J. Gotelli and G. R. Graves, *Null Models in Ecology* (Smithsonian Institution Press, Washington, DC, 1996).
7. P. H. Harvey, R. K. Colwell, J. W. Silvertown, R. M. May, *Annu. Rev. Ecol. Syst.* **14**, 189 (1983); D. R. Strong Jr., D. Simberloff, L. G. Abele, A. B. Thistle, *Ecological Communities: Conceptual Issues and the Evidence* (Princeton Univ. Press, Princeton, NJ, 1984).

PERSPECTIVES: VOLCANISM

Will Vesuvius Erupt? Three Million People Need to Know

Grant Heiken

The Bay of Naples and the adjacent Campanian Plain are rich, the seaside beautiful, and the weather mild. During the time of the Roman empire, this region was a prime location for holiday villas, and during the 18th and 19th centuries, Naples was a required destination on the "Grand Tour" for well-educated, wealthy youths. But the region has also been the site of devastating volcanic eruptions, most notably that of 79 A.D., which buried the thriving Roman town of Pompeii. Today, close to 3 million people live in the volcanic areas around Naples, 1 million of them on the slopes of Mount Vesuvius. Historic and geological records and seismic monitoring networks are now providing insights into the patterns of volcanic activity and may help mitigate the hazards of future eruptions.

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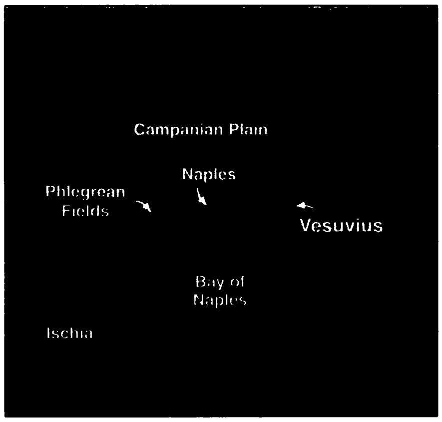
Neapolitans are well aware of the area's volcanic heritage and are periodically reminded of the potential danger under which they live. In 1982–84, ground uplift and earthquakes in the Phlegrean Fields (see the figure on this page) resulted in the evacuation of thousands of residents from the nearby city of Pozzuoli. When the uplift and seismic activity ceased, the political response was violent and chaotic, including accusations aimed at the scientists for "crying wolf." But after the events in the Phlegrean Fields, the Italian National Research Council's National Group of Volcanology and the Ministry for Civil Protection expanded their research effort to better understand the eruption histories of Neapolitan volcanoes. Improved monitoring systems at the Osservatorio Vesuviano (OV) (*1*) were established, along with an intense educational campaign focusing on volcanic eruptions and associated hazards for the region's cities. Scientists are asked tough questions by the public, such as, when will Vesuvius erupt? How will it erupt? And which areas will be affected? These questions are extremely difficult to answer and are best addressed by studying past eruptions and establishing an integrated monitoring network.



Satellite image of the Bay of Naples.

Volcanologists from the OV and the Universities of Naples and Pisa have used data from outcrops and drill holes to evaluate the Plinian (explosive) and Strombolian (lava fountains and lava flow) volcanic activity in the area of the Bay of Naples that began 126,000 years ago. During the past 19,000 years, seven Plinian eruptions have occurred, at 18,300, 16,780*, 8010, 3360, 1920 (79 A.D.), 1527*, and 368* years before the present (an asterisk denotes smaller scale Plinian eruptions) (*2–4*). These eruptions each produced between 5 and 11 km^3 of volcanic ash and pumice that were deposited as fallout or fast-moving density currents known as pyroclastic flows or surges. Each eruption devastated an area of 20,000 to 30,000 hectares, and some of the currents extended as far as 22 km beyond the crater. Plinian eruptions pose the greatest hazard to people living on or near Vesuvius because the 600°C density currents are capable of flattening 3-m-thick stone walls 10 km from the vent. In almost all of these explosive eruptions, exsolution of gases from rising magma was followed by pressure release within 2 km of the surface, magma fragmentation, and eruption. As the eruption progressed, the fragmentation process was enhanced when water and magma mixed in limestone aquifers underlying the volcanic and sedimentary deposits of the Campanian Plain (see the figure on this page). Thermally altered fragments from the limestones were also erupted, indicating that increased explosive fragmentation, perhaps associated with magma/water mixing, occurred below a depth of 2 km. At the same time as the Plinian eruptions, a caldera (collapse crater), now called Monte Somma, was formed.

Since 79 A.D., Strombolian activity has constructed the summit cone that today partly fills the Monte Somma. Periods of Strombolian activity—more common than Plinian eruptions yet less dangerous—have occurred frequently since 1631 A.D. (see the figure on the next page). There were 18 eruption cycles between 1631 and 1944 alone, ranging from 2 to 37 years, with repose periods of 0.5 to 6.8 years between cycles (*3*). Since 1944, Vesuvius has seen no activity except fumaroles in the summit crater. This unusually long repose period of 55 years may indicate dormancy or the quiet time preceding a Plinian eruption. To de-

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