Ecological Experiments with Model Systems

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Some of the classic experiments in ecology have involved real organisms interacting in the laboratory, that is, model systems. Ecologists are increasingly using model systems to investigate problems of global environmental change and questions about the assembly, persistence, and stability of complex communities. Model laboratory systems are a halfway house between mathematical models and the full complexity of the field, and they yield powerful insights into the dynamics of populations and ecosystems.

Ecologists have always used model systems to disentangle the complexities of nature (*1*). Examples of such systems range from the simplicity of experimentally sown mixtures of two species of plants (*2*) to sophisticated controlled environment facilities housing entire, but artificially created, terrestrial ecosystems (*3, 4*) (Fig. 1). Here I review a range of questions that ecologists have examined using model laboratory systems, point out the strengths and weaknesses of the approach, summarize major results, and assess future applications. I have primarily restricted attention to systems involving two or more species over several generations, in which the interactions between organisms, and between organisms and their environment, persist without the repeated intervention of the experimenter. For other reviews, see (*5–8*).

Experiments with model laboratory systems lie on a continuum of approaches that ranges from mathematical models to whole-ecosystem studies. Each approach has its advantages and disadvantages; none are intrinsically superior. For example, a comparison of the behavior of small artificial and large field ecosystems may reveal that fundamentally similar processes are at work, or it may reveal important differences in behavior (*9*). The differences are as important as the similarities, because they sharpen understanding of the role of scale in ecology. Among the major advantages of model systems is the ease with which the experiment can be replicated and the parameters of the experiment manipulated; obvious disadvantages of model systems include their small size and (frequently) their biological and structural simplicity.

Historical Perspective

Some of the classic studies in ecology have been carried out with model laboratory systems. Experimental and theoretical work by Gause with three species of *Paramecium* (*10*) remains a textbook example of competitive exclusion and coexistence. Gause's work had a seminal influence on field studies of bird assemblages (*11, 12*) and has spawned a vast literature. Equally well known are Park's (*13*) laboratory studies on *Tribolium* flour beetles which demonstrated the effects of chance, climate, and a sporozoan parasite on the outcome of two-species competition. Despite the clear demonstration in Park's work of the significance of two species sharing an enemy, the consequences of this situation remained neglected by all but a few ecologists (*14, 15*) until recently. Park's results are now receiving increasing attention, both theoretically and in laboratory and field systems (*16*).

Interactions involving one species of enemy and one species of victim (predator and prey or parasitoid and host) have been reasonably well studied in the laboratory. Although it is now well known that different parameter values can give rise to markedly different population dynamics in structurally similar models, Utida (*17*) appears to have been among the first to recognize this, linking differences in the dynamics of long-running populations of bean weevils (*Callosobruchus*) to differences in the fecundities and searching efficiencies of two species of parasitoids.

Huffaker's work with *Eotetranychus* mites as prey and *Typhlodromus* mites as predators (*18*) remains the classic experimental demonstration of how environmental heterogeneity, generating spatial refuges, allows the persistence of an otherwise unstable predator-prey interaction. Huffaker also concluded that local dispersal from adjacent, occupied patches was a key to the persistence of the system. Only relatively recently have sufficiently powerful computers made it easy for ecologists to model the spatial dynamics of coupled enemy-victim populations with local movement (*19*). These models confirm that local movement in a patchy environment can stabilize an otherwise unstable enemy-victim interaction. They also show that deterministically generated spatial patterns in such populations can be exceedingly complex, as Huffaker's mites indeed demonstrated. There is clearly considerable potential in this area for further integration of theory with experimental work by using model laboratory systems.

Trophic, competitive, and mutualistic interspecific interactions are fundamental to all ecological systems. It is curious that the majority of simple (two to three species) laboratory models involve either competition or predator-prey and parasitoid-host interactions. I know of no studies on the long-term dynamics of a higher land plant and an herbivore, even though there are important differences between such systems and "traditional" predator-prey interactions (*20*); animals certainly affect plant population dynamics in the short-term in laboratory systems (*21*) and may have long-term impacts. Efforts to study long-term population dynamics of mutualists using simple (two to three species) model systems also appear to be lacking, although mycorrhizae have been shown to modulate plant community dynamics in relatively species-rich laboratory assemblages (*22, 23*) (see be-

Fig. 1. A model terrestrial ecosystem with up to 40 species of plants, herbivores, parasitoids, and decomposers housed in one of 16 replicate chambers in the Ecotron facility (*3, 4*). [Photograph COI/CPB]

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low). The concentration of research on competitive and predator-prey interactions in simple model systems may have as much to do with academic traditions within different subdisciplines of ecology as it has with the inherent difficulties of working on different kinds of systems.

A quite separate tradition in ecology has involved the use of small aquatic assemblages to investigate emergent properties of communities and ecosystems (*5*, *24*). Examples range from closed containers requiring only sunlight to sustain them, to more complex, open chemostats. This work has clarified a number of issues about productivity, metabolism, nutrient cycling, and succession in intact ecosystems [see for example (*24*)]. A weakness of this approach is its predominantly holistic view of nature, implicitly (and sometimes explicitly) viewing ecosystems as homeostatic superorganisms with "goals" and "strategies" (*25*). In so doing, this approach fails to exploit one of the real advantages of model systems, which is the ability to dissect component parts and reveal mechanisms.

Global Change and Controlled Environment Facilities

Paradoxically, despite the small spatial scale of many systems (none are larger than a few square meters), the last decade has seen a rapid rise in the use of controlled environment facilities (CEFs) (Figs. 1 and 2) to study the consequences of global environmental change for terrestrial ecosystems. Enhanced temperatures, CO_2, and ultraviolet (UV-B) light and the loss of biodiversity are easier, and frequently cheaper, to manipulate in a CEF than in the field. Work on global change in CEFs takes a variety of forms (*6*) and seems likely to increase dramatically in the next few years.

My colleagues and I have used the Ecotron (*3*, *4*) to simulate the effects of loss of biodiversity on ecosystem processes. Species were assembled so that lower diversity communities resembled depauperate descendants of higher diversity communities that had lost species uniformly from all trophic categories. Most ecosystem processes varied significantly with species richness, but not in any systematic way. Whole-ecosystem uptake of CO_2 and plant productivity, however, both declined as species richness declined. Overall, the data supported three of four possible theoretical relations between diversity and ecosystem function (*26*) and provided the first experimental evidence that species richness affects ecosystem processes (*27*).

The effects of rising atmospheric concentrations of CO_2 on terrestrial ecosystems are potentially complex [see also (*9*)], ranging from increases in photosynthetic rates, which may affect plant abundances, to effects on root exudates and mycorrhizas on the one hand and insect herbivores on the other.

Bazzaz and colleagues (*28*) carried out pioneering investigations on the consequences of rising global atmospheric CO_2 concentrations for the structure and dynamics of successional annual plant communities maintained in a glass house. This substantial body of work shows that different species of plants are differentially sensitive to enhanced CO_2, which can alter growth rates, biomass allocation patterns, and reproductive outputs. In general, C_3 plants are more sensitive than C_4 plants. Precise, quantitative predictions of the consequences of these changes for the long-term composition of plant communities will not, however, be easy; not only do plant species differ in their sensitivity to CO_2, but their responses are modulated by nutrients, water, and temperature (all of which will be affected by climate change) and by interactions with competitors (*28*). But there is no doubt that rising global concentrations of atmospheric CO_2 will change the relative abundances and species composition of some terrestrial plant communities.

There may possibly be signs of such effects on long-term study plots in tropical forests (*29*), manifest by an increasing rate of turnover in trees and in the growth of lianas. These trends appear to have accelerated since 1980. Intriguingly, it has proved possible to simulate the effects of rising CO_2 concentration on miniature (7-m^2) humid forest ecosystems, housed in a CEF in Switzerland (*30*). In these experiments fine-root production and soil respiration both increased under elevated CO_2, but there were no significant effects on stand biomass. In part this may be because the experiment lacked statistical power (there were only two replicates per treatment). Alternatively, it may be because woody tropical forest plants do not respond to rising CO_2 concentrations in the same way as herbaceous annuals. This highlights one problem with experiments in CEFs: Because of their size and speed of development, it is easier to work with annual plants (*4*, *7*, *28*) than with larger, longer lived species. It is still unclear how easily results can be extrapolated between plants from very different functional groups. Theory and data suggest that simple extrapolation is unwise (*31*).

An additional complication, again revealed by work with plant communities in a CEF, is that elevated CO_2 concentrations can cause an increase in the eflux of carbohydrates from roots to soil (*23*, *30*), with differential consequences for mycorrhizal and nonmycorrhizal species of plants, through effects on soil microbial communities and nitrogen dynamics (*23*). CEFs appear to be a particularly appropriate means of investigating these complex and interrelated processes, because the species composition, nutrient status of the soil, and major fluxes can all be manipulated and measured (*7*).

Changes in the carbohydrate dynamics

Fig. 2. Solardomes, geodesic hemispheres with an internal airspace that has simple aerodynamic properties, used by ecologists at Lancaster University, United Kingdom, to house model systems for research on the affects of atmospheric pollutants and enhanced CO_2 concentrations on plant and insect populations (*46*). [Photograph by Ruth Berry]

of plants resulting from elevated CO_2 atmospheres can also be important in aboveground processes, through changes in the carbon-to-nitrogen ratios of foliage, with potential consequences for insect (and other) herbivores. Some of the earliest work on the effects of elevated CO_2 on plant-herbivore interactions was performed in the CEF known as the Phytotron at Duke University in North Carolina. *Pseudoplusia* caterpillars increased consumption rates by 20 to 81% on host plants (*Glycine*) grown in an elevated CO_2 atmosphere (*32*). This response is now known to be frequent (though not universal) in lepidopteran larvae, allowing them to maintain growth rates despite the reduced quality (lower foliage nitrogen) of plants grown in high CO_2 (*30, 32*). The full implications of these studies for plant-herbivore interactions in the next century are still unclear (*33*), but they are unlikely to be negligible. The potential for using CEFs to study the dynamics of phytophagous insect populations over several generations under various global-change scenarios is obvious.

Assembly Rules and the Dynamics of Complex Systems

There can be no herbivores without plants, but are there less trivial assembly rules for ecological systems? For example, are some food web configurations more likely to persist than others (*8, 34*)? Must species-rich communities be built up through particular subsets of species, and are there forbidden combinations and alternative stable states along that route (*35*)? How does the environment interact with the biota to determine community diversity and dynamics (*36*)? The first steps toward answering these questions are the small, two- and three-species systems discussed earlier. These "modules" form the units from which larger communities are assembled; theory tells us that combining modules into more complex webs may fundamentally change the dynamics of the component species (*16, 17, 37*).

The use of model systems to study community assembly is a relatively new field. In an early experiment (*38*) aquatic microcosms were repeatedly inoculated with several species of crustacea and algae. After ~250 days, the 15 replicate communities each contained the same five algae, three cladocera, and one amphipod; all other taxa failed to establish (Fig. 3). Lacking are theoretical predictions about which species would and would not be able to coexist in the system; indeed, sufficiently detailed models may still be some way off, although an appropriate framework now exists (*39*). But Neill's work clearly demonstrates the existence of stable combinations of species and the exclusion of others [although convergence on the same species combinations is not an inevitable outcome (*40*)].

Recent work by Lawler and Morin (*8*) is starting to chip away at mechanisms in food web assembly. Theory predicts (*8, 34*) that long food chains, and those with abundant omnivory (species feeding on more than one trophic level), are less likely to be stable than shorter, simpler webs. Model food webs of bacteria, bacterivorous protists, and predatory protists support the first prediction but refute the second (*8*). A second set of experiments confirm model predictions about prey coexistence with shared predators (*16*). This work is now being extended to study the relative strengths of "top-down" (predation) versus "bottom-up" (nutrient) effects in food chains (*9, 41*).

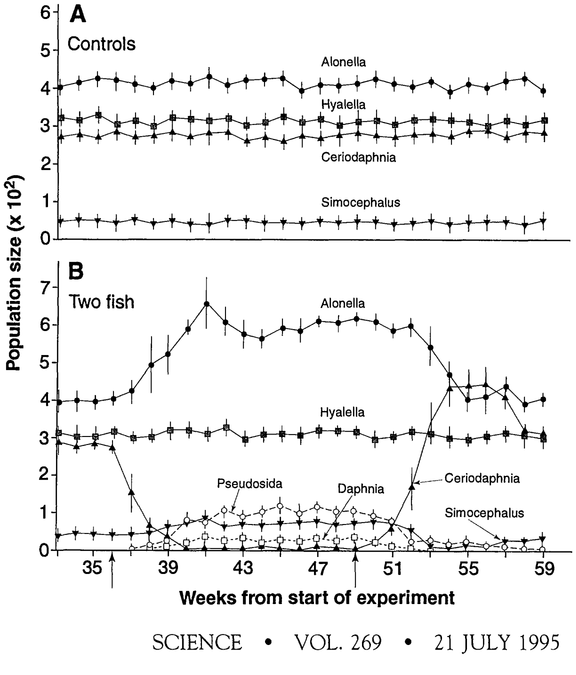

Fig. 3. The result of repeatedly inoculating aquatic microcosms (crystallizing bowls maintained in a CEF) with 12 species of crustaceans and more than 20 green and blue-green algal species. After 35 weeks, the 15 replicate communities each contained the same five algae and four crustaceans (three cladocerans and one amphipod). (**A**) The very stable dynamics of the cladocerans and amphipod in five of these microcosms over the ensuing 25 weeks. (**B**) The dynamics of five microcosms subject to regular predation by two small fish between weeks 36 and 49 (time period indicated by arrows on the abscissa), which allowed two additional crustaceans to colonize (*38*).

Two current concerns (*42*)—the roles of chance and history in determining contemporary community structure, and the interplay of local and regional processes—have been addressed by Drake and colleagues (*35*). They used a unique model landscape, consisting of interconnected 1-liter aquatic microcosms, through which an assemblage of four algal species and four crustacea invade and spread. By the end of the experiment (80 days), species were distributed heterogeneously among patches (recall Huffaker's experiment) and had converged on one of several alternative states (defined by species' presence-absence and relative dominance), despite identical initial conditions. A naïve investigator, unfamiliar with the history of the system, might seek to explain the differences between patches by deterministic differences in their environment; they would, of course, be wrong. It is a moot point, however, whether these differences would have persisted had the system been run for longer (*43*).

Although the majority of recent laboratory studies of community assembly use aquatic systems (probably because of the short generation times of the organisms involved), there is no reason in principle why terrestrial communities cannot be similarly investigated (*7*). A good example is the importance of variation in early spring weather for the structure of the annual plant communities of the eastern United States; the responses are predictable from a knowledge of the physiological ecology of seed germination (*44*). Using a similar approach with laboratory communities of British herbaceous plants, Grime *et al.* (*22*) demonstrated that both mycorrhizal infection and grazing promoted diversity, whereas soil heterogeneity did not. As they point out, "all three have been implicated in diversity theories by earlier investigators, but the effects of each are exceedingly difficult to quantify in natural vegetation."

The potential is enormous for studying processes in the laboratory that are simply too difficult, too time consuming, or too expensive to do in the field. As one final example, the quickest though certainly not the only way to obtain sufficiently long time series to discover whether complex ecological systems display chaotic dynamics (*1, 45*) is to assemble and run communities of the desired complexity in a CEF, with or without imposed environmental "noise." A similar experiment in the field with birds or fish or higher plants might take on the order of 1000 years.

Concluding Remarks

Model laboratory systems are an ecological tool. Like all tools they do some things well, some things badly, and other things not at all. At worst, they are analogs of how we imagine nature to work, not how it actually works. At best, the task of assembling, maintaining, and predicting the behavior of even moderately complex ecosystems in the laboratory tests our understanding to the limit (*7*). More than anything else, model systems act as a bridge between theory and nature (*1*). They are not a substitute for studying the real thing, but by simplifying the complexities of nature, model systems can sharpen our understanding of natural processes.

The next decade is likely to see a big increase in the use of model laboratory systems in ecology. The trend is toward more complex and more realistic assemblages. The majority of studies to date have built communities from the bottom up, by the introduction of species into an abiotic environment. But an alternative is to move the field, as buckets of water or intact blocks of soil, complete with biota, into a CEF, blurring still further the already fuzzy distinctions between laboratory microcosms, mesocosms maintained outdoors, and field manipulation experiments.

The advantages of model laboratory systems for ecology are replicability, reproducibility, mastery of environmental variables, ease of manipulation, and control over who enters the ark. Because they can involve creatures with short generation times and usually run without seasons, model systems also speed up nature. Claimed disadvantages include their taxonomic and structural simplicity, lack of spatial and temporal heterogeneity, small physical size, and concerns about whether organisms that thrive in microcosms and mesocosms are representative of those that do not. Some of the things that model laboratory systems are not good at are well described by Carpenter *et al.* (*9*). These criticisms and problems matter if we blindly extrapolate from the laboratory to the field. They do not matter if we treat the problems as research questions (*7*): What differences do size, simplicity, or lack of seasonality make to ecological processes? And these criticisms are irrelevant if we see model systems as one part of a rich, interrelated web of approaches to understanding and predicting the behavior of populations and ecosystems.

REFERENCES AND NOTES

1. P. Kareiva, in *Perspectives in Ecological Theory*, J. Roughgarden, R. M. May, S. A. Levin, Eds. (Princeton Univ. Press, Princeton, NJ, 1989), pp. 68–88.
2. C. T. de Wit, *Versl. Landbouwkd. Onderz.* **660**, 1 (1960).
3. S. Naeem *et al.*, *Nature* **368**, 734 (1994).
4. S. Naeem *et al.*, *Philos. Trans. R. Soc. London Ser. B* **347**, 249 (1995).
5. R. J. Beyers and H. T. Odum, *Ecological Microcosms* (Springer-Verlag, Berlin, 1993).
6. C. Körner, J. A. Arnone III, W. Hilti, in *Design and Execution of Experiments in CO_2 Enrichment. Ecosystems Research Report 6*, E.-D. Schulze and H. A. Mooney, Eds. (Commission of the European Communities, Brussels, 1993), pp. 185–198.
7. J. H. Lawton, *Ecology*, in press.
8. P. J. Morin and S. P. Lawler, in *Food Webs: Integration of Patterns and Dynamics*, G. A. Polis and K. Winemiller, Eds. (Chapman and Hall, New York, 1995), in press.
9. S. R. Carpenter, S. W. Chisholm, C. J. Krebs, D. W. Schidler, R. F. Wright, *Science* **269**, 324 (1995).
10. G. F. Gause, *The Struggle for Existence* (Williams and Wilkins, Baltimore, MD, 1934).
11. D. Lack, *Darwin's Finches* (Cambridge University Press, Cambridge, 1947).
12. R. H. MacArthur, *Ecology* **39**, 599 (1958).
13. T. Park, *Science* **138**, 1369 (1962).
14. M. H. Williamson, *Nature* **180**, 422 (1957).
15. R. D. Holt, *Theor. Popul. Biol.* **12**, 197 (1977).
16. ——— and J. H. Lawton, *Annu. Rev. Ecol. Syst.* **25**, 495 (1994).
17. S. Utida, *Cold Spring Harbor Symp. Quant. Biol.* **22**, 139 (1957).
18. C. B. Huffaker, *Hilgardia* **27**, 343 (1958).
19. M. P. Hassell, H. N. Comins, R. M. May, *Nature* **370**, 290 (1994).
20. M. J. Crawley, *Herbivory. The Dynamics of Animal-Plant Interactions* (Blackwell Scientific, Oxford, 1983).
21. L. Thompson *et al.*, *Oecologia* **95**, 171 (1993).
22. J. P. Grime *et al.*, *Nature* **328**, 420 (1987).
23. S. Díaz *et al.*, *ibid.* **364**, 616 (1993).
24. E. P. Odum, *Science* **164**, 262 (1969).
25. B. A. Manson and J. M. McGlade, *Oecologia* **93**, 582 (1993).
26. E.-D. Schulze and H. A. Mooney, Eds., *Biodiversity and Ecosystem Function* (Springer-Verlag, Berlin, 1993).
27. P. R. Ehrlich and E. O. Wilson, *Science* **253**, 758 (1991).
28. F. A. Bazzaz, *Annu. Rev. Ecol. Syst.* **21**, 167 (1990).
29. O. L. Phillips and A. H. Gentry, *Science* **263**, 954 (1994).
30. C. Körner and J. A. Arnone III, *ibid.* **257**, 1672 (1992).
31. J. P. Grime, J. G. Hodgson, R. Hunt, *Comparative Plant Ecology: A Functional Approach to Common British Species* (Unwin Hyman, London, 1988).
32. D. E. Lincoln, E. D. Fajer, R. H. Johnson, *Trends Ecol. Evol.* **8**, 64 (1993).
33. J. H. Lawton, in *Insects in a Changing Environment*, R. Harrington and N. E. Stork, Eds. (Academic Press, London, 1995), pp. 3–26.
34. S. L. Pimm, J. H. Lawton, J. E. Cohen, *Nature* **350**, 669 (1991).
35. J. A. Drake *et al.*, *J. Anim. Ecol.* **62**, 117 (1993).
36. L. S. Luckinbill and M. M. Fenton, *Ecology* **59**, 1271 (1978).
37. M. E. Hochberg, M. P. Hassell, R. M. May, *Am. Nat.* **135**, 74 (1990).
38. W. E. Neill, *Ecology* **56**, 809 (1975).
39. R. D. Holt, J. Grover, D. Tilman, *Am. Nat.* **144**, 741 (1994).
40. U. Sommer, *Oecologia* **87**, 171 (1991).
41. D. Balčiūnas and S. P. Lawler, *Ecology* **76**, 1327 (1995).
42. R. E. Ricklefs and D. Schluter, Eds., *Species Diversity in Ecological Communities. Historical and Geographical Perspectives* (Univ. of Chicago Press, Chicago, IL, 1993).
43. J. P. Grover and J. H. Lawton, *J. Anim. Ecol.* **63**, 484 (1994).
44. F. A. Bazzaz, *Plants in Rapidly Changing Environments: Linking Physiological, Population, and Community Ecology* (Cambridge Univ. Press, Cambridge, 1995).
45. A. Hastings *et al.*, *Annu. Rev. Ecol. Syst.* **24**, 1 (1993).
46. P. W. Lucas, L. Rantanen, H. Mehlhorn, *New Phytol.* **124**, 265 (1993).
47. I am extremely grateful to F. Bazzaz, M. Crawley, J. Drake, D. Ebert, C. Godfray, A. Gonzales, P. Grime, M. Hassell, P. Heads, H. Jones, C. Körner, S. Lawler, T. Mansfield, P. Morin, O. Petchey, J. Reynolds, L. Thompson, and M. Williamson for providing references, reprints, and preprints, and for comments on the manuscript.

Landscape Ecology: Spatial Heterogeneity in Ecological Systems

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Many ecological phenomena are sensitive to spatial heterogeneity and fluxes within spatial mosaics. Landscape ecology, which concerns spatial dynamics (including fluxes of organisms, materials, and energy) and the ways in which fluxes are controlled within heterogeneous matrices, has provided new ways to explore aspects of spatial heterogeneity and to discover how spatial pattern controls ecological processes.

Landscape ecology is the study of the reciprocal effects of spatial pattern on ecological processes (*1*); it promotes the development of models and theories of spatial relations, the collection of new types of data on spatial pattern and dynamics, and the examination of spatial scales rarely addressed in ecology. Throughout much of its history, ecology sought or assumed spatial homogeneity for convenience or simplicity; scales that lent an apparent uniformity to the processes under study were emphasized, and heterogeneity was taken as a necessary evil or an unwelcome complication. In contrast, landscape ecology regards spatial heterogeneity as a central causal factor in ecological systems, and it considers spatial dynamics and ecology's founding concern with the temporal dynamics of systems to be of equal importance. Factors in temporal dynamics include population growth and regulation, community dynamics or succession, and the dynamics of evolutionary change. The spa-

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