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The role of experimental microcosms in ecological research

Lauchlan H. Fraser and Paul Keddy

A number of recent and important developments in community ecology have been derived from experiments conducted in microcosms. Studies with microcosms have addressed a broad range of phenomena, including climate change, biodiversity, assembly rules, habitat restoration, trophic dynamics and mycorrhizal associations. The common factor linking these studies is that they manipulate an individual environmental axis and explore the role that axis plays in structuring communities. We discuss six recent studies to illustrate the use and design of microcosms for community ecology research.

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Microcosms are small ecosystems in containers. They can range from simple experimentally sown mixtures of two species of plants (for example, de Wit's[1] replacement series) to sophisticated controlled environments housing entire terrestrial ecosystems such as the Ecotron[2]. Microcosms also vary in size from test-tube studies[3] to the vast multi-ecosystem complex constructed in Arizona (Biosphere 2)[4]. The main role of microcosms, also called model systems, is to act as a bridge between theory and nature – they can increase our understanding of natural processes by simplifying the complexities of our natural environment[5]. Gause's[6] pioneering work on competitive exclusion, Huffaker's[7] spatial predator–prey models and Park's[8] flour beetle competition experiments are classic examples of microcosm use. A number of recent studies that use microcosms include: (1) the effects of elevated CO_2 on a plant community[9]; (2) biodiversity effects on community factors[10]; (3) assembly rules for a wetland plant community[11]; (4) effects of microtopographic heterogeneity and seed propagule source on floristic diversity[12]; (5) top-down control from carnivores and its effect on plant community composition[13]; and (6) the effects of mycorrhizae on plant community composition[14]. The early studies explored population ecology principles, while the later studies explored community and ecosystem ecology.

Advantages of using microcosms include ease of replication, precise control over environmental variables, and the power to manipulate the parameters and treatments under investigation[15,16]. Limitations and disadvantages are restricted space and over-simplification[17,18].

Limnologists, toxicologists and microbiologists[19] have used microcosms as a powerful research tool, but they have been relatively neglected by terrestrial community ecologists (Table 1). The total number of published microcosm/mesocosm experiments has doubled in the past seven years and this has been reflected in the large increase in review papers. To illustrate the application of microcosms as an important research tool in terrestrial community ecology we will explore six studies, and highlight some common threads among them.

  0169-5347/97/$17.00 PII: S0169-5347(97)01220-2 *TREE vol. 12, no. 12 December 1997*

Elevated CO_2 effects on a plant community

Diaz *et al.*[9] tested the community level response of plants to elevated CO_2. There were marked differences in the responsiveness of native British plant species to CO_2 concentration. However, the pattern of response differed substantially from that recorded for plants grown in the laboratory as isolated individuals. Their results suggest that there may be a feedback mechanism in which elevated carbon dioxide causes an increase in substrate release into the rhizosphere by non-mycorrhizal plants [*Rumex obtusifolius* (broad-leaved dock) and *Cardamine flexuosa* (wavy bitter-cress)], leading to mineral nutrient sequestration by the expanded microflora and a consequent nutritional limitation on plant growth. As a result, slow-growing mycorrhizal plants [*Agrostis capillaris* (common bent) and *Calluna vulgaris* (heather)] begin to dominate after 112 days. Factors which were very difficult to control and measure in the field could be examined through the use of microcosms, although the short duration of time places constraints upon the conclusions that we can draw.

Table 1. Summary of published papers listed in *Biological Abstracts* with the words microcosm or mesocosm in the title or abstract from 1990–1996

	1990	1991	1992	1993	1994	1995	1996
Limnology	19	13	17	23	28	39	28
Toxicology[a]	17	15	13	23	27	35	35
Microbiology	17	18	23	24	33	51	27
Terrestrial (pop.)	0	2	2	2	1	7	3
Terrestrial (comm.)	0	0	0	0	1	3	5
Review	2	0	0	1	1	4	7
Total	55	48	55	73	91	139	105

[a]Many of the toxicology experiments were conducted in aquatic systems, but if a pollutant was being investigated it was deemed to be toxicology.

Biodiversity and ecosystem function

In their Ecotron experiments, Naeem *et al.*[10] tested for an effect of biodiversity upon five ecosystem processes: (1) community respiration; (2) decomposition; (3) nutrient retention; (4) plant productivity; and (5) water retention. They found that declining biodiversity could alter the function, or 'performance', of ecosystems. Specifically, both CO_2 consumption (measured in relation to community respiration) and plant productivity were higher in higher-diversity communities.

Assembly rules for a wetland plant community

Weiher and Keddy[11] conducted a large, long-term microcosm study to explore the principle of assembly rules[20]. Assembly rules are the constraints that act on a common species pool to determine the actual composition of a community. Environmental factors, including fertility, water depth, fluctuations in water depth, soil texture, leaf litter, length of the initial growing season, and invasion by *Typha* (cat-tail), were manipulated to determine how a common plant species pool would be differentially effected over five years. At the end of the period, there were strong and consistent effects of water level, fertility and leaf litter (in decreasing order of importance) on community composition, with lesser effects of sowing time. The resulting community assembly was modelled as a series of environmental filters.

Microtopographic heterogeneity and floristic diversity in wetlands

Vivian-Smith[12] manipulated soil topography (flat surface versus hummock-hollow) in combination with three propagule sources (seed bank, seeds, seed bank + seeds) to determine their combined effect on floristic diversity. She determined that community composition, abundance of individuals and above-ground biomass responded differentially to heterogeneity and propagule source. Most species achieved greater abundance in heterogeneous environments. Furthermore, most species within the heterogeneous environment showed distinct habitat preferences for hummock or hollow microhabitats, with many of the rarer species favouring hummocks.

Tritrophic interactions and their effect on plant species composition

Fraser and Grime[13] investigated tritrophic interactions (ladybird–aphid–grass) at high and low soil fertility. The grass community consisted of three functionally different species (fast-growing annual; fast-growing perennial; and slow-growing perennial), which are thought to be differentially palatable to herbivores[21,22]. At low soil fertility, plant biomass was low, aphid numbers were small, and ladybird activity was minimal. At high soil fertility, top-down control from the ladybirds indirectly caused a significant response in plant biomass and species composition. The fast-growing annual 'benefited' from the presence of ladybirds, while the slow-growing grass suffered. The opposite was found when ladybirds were absent but aphids present. These results suggest that top-down control of herbivory may have important consequences on plant species composition in high productivity communities. The separation of trophic interactions that was done in this experiment is virtually impossible to accomplish in the field.

Mycorrhizal effects on plant community composition

Wilson and Hartnett[14] examined the functional significance of mycorrhizal infection on plant growth and dynamics of an assemblage of eight tallgrass prairie grass and forb

Table 2. Summary of the experimental design of each of the six case studies reviewed

	No. of species						
Source	Plants	Animals	No. of trophic levels	No. of replicates	No. of treatments	Volume (l)	Duration of study
Diaz *et al.*[9]	n[a]	0	1	6	4	90	112 days
Naeem *et al.*[10]	2	7	4	4			
	5	10	4	4	3	8800	206 days
	16	15	4	6			
Weiher and Keddy[11]	20	0	1	5	24	70	5 years
Vivian-Smith[12]	19[a]	0	1	5	6	40	1 year
Fraser and Grime[13]	3	2	3	6	6	1800	217 days
Wilson and Hartnett[14]	8	0	1	16	2	66	294 days

[a]Natural seed bank.

Box 1. Guidelines for the design of a community-level microcosm experiment

- **What is the question?** There are many unanswered questions in ecology; a fundamental challenge is to distinguish between trivial and significant questions[30] (Keddy[25] offers some proposed guidelines). Once the question is clear, the choice of the right approach becomes more obvious.
- **Kind of treatments.** Community ecology involves the search for the processes that structure plant and animal communities. In choosing treatments, consider those factors that are most important and therefore offer the broadest possible generality. Examples include resource levels, environmental constraints, and presence or absence of factors such as herbivores or mycorrhizae.
- **Species.** Real communities have many species, and the more used in a study, the greater the realism. The numbers of species included in each of the case studies is always greater than five, and, in some cases, more than one trophic level is examined.
- **Comparative approach.** Some species share similar traits and can be grouped in guilds, strategies or life-history types. In other cases quantitative, screened, trait data, such as relative growth rates or relative competitive ability, make it easier to both interpret results and draw meaningful generalizations from them[31]. We therefore recommend a comparative approach to species selection.
- **Replication.** The number of treatments places a potential limit on the number of replicates: more treatments means fewer replicates if the number of microcosms available is finite. Mead[32] discusses the issues involved in deciding upon the number of replicates: (a) the resources available; (b) the variability of experimental units; (c) the treatment structure; (d) the size of effect which is of importance; and (d) the relative importance of different comparisons. For general purposes, three replicates is the absolute minimum, but since community analyses are complex it is important to increase replication whenever possible.
- **Size.** The size of the microcosms will be related to the size of the study organisms, the number of species included, and, to some extent, the treatments. In this case, bigger is not necessarily better, but we recommend areas no smaller than 25 × 50 cm for most purposes.
- **Duration.** The duration of the study depends on the ecological processes under investigation and the life histories of the species. Naeem *et al.*[10] used short-lived ephemeral species and therefore the relatively short period of 206 days was adequate because it represented the life cycle of the organisms. Weiher and Keddy[11] used a broad range of plant life history types, which included slow-growing perennials, necessitating five years of study. Microcosms are not suited to long-term studies (>5 years). Although long-term studies are essential for the development of ecology, limitation of space in microcosms mean that the artificial constraints created by the investigator (e.g. limitations on rooting depth, metapopulation processes, territoriality, inputs and outputs, natural disturbances, seasonality) will usually exceed the benefits of continuing the work.

species. The suppression of mycorrhizal infection resulted in a 31% reduction in total net aboveground plant production as well as changes in the relative production of C_4 and C_3 plants. The C_4 tallgrasses produced less plant biomass, whereas the C_3 grasses produced more biomass and were a significanlty greater proportion of total community biomass in mycorrhizal-suppressed microcosms. Forbs showed variable responses to the mycorrhizal treatment, but the two legumes had significantly lower survivorship in the mycorrhizal-suppressed microcosms.

How to design a community-based microcosm experiment

Table 2 summarizes the functional points in each of the above case studies. The studies seem to differ dramatically in their objectives, but there is a common thread: all of them have been designed to manipulate an individual environmental axis (e.g. CO_2, diversity, water level fluctuations, microtopography, trophic interactions, fertility, mycorrhizae) and explore the role that axis plays in structuring communities. By necessity, all the studies contain multi-species assemblages because they all have the objective of determining the impact of an independent variable on the community. Further factorial experiments can explore combinations of factors and separate complex causal relationships. Comparison of these studies suggests some general guidelines for the construction of microcosm studies (Box 1).

Top-down and bottom-up reduction applied to community ecology

These kinds of experiments provide an important but misunderstood tool for the analysis of ecological communities. To appreciate their value, we need to consider the holism–reductionism spectrum in community ecology. Generally, holists are concerned with how parts are organized to create wholes, and the rules that are used to assemble the parts that create the whole. On the other hand, reductionists believe that the analysis of these parts will reveal the mechanism of the phenomenon. A range of views can be found elsewhere[17,23–25]. Microcosms provide a way of working across the spectrum.

The simple distinction between holism and reductionism is inadequate to describe the strategic and tactical opportunities available to us. We can use top-down reduction, for example, by creating natural gradients, or by eliminating a component like mycorrhizae[14,26], or an entire trophic level[13,27]. We are then using a treatment factor like a sword to slice through the variation in nature. Take, for illustration, the case study above where 20 plant species were used to form a pool upon which filters acted[11]. Here, the emphasis was upon using the particular set of species to represent an array of functional types, and their organization by several gradients which are known to be important in nature. Alternatively, microcosms can also be used to explore ecosystem processes which may require a bottom-up assembly of the community. For example, the Ecotron experiment included a diversity treatment with three levels where the number of species was successively increased[10]. The lower-diversity communities were a subset of its higher-diversity counterpart and, yet, all community types had four trophic levels.

Thus, microcosms are an important tool for escaping the holism–reductionism dichotomy. They intersect naturally with field experiments such as the Park Grass Experiments[28] in providing a top-down reduction of nature. Furthermore, by providing a way to design orthogonal gradients and treatments, they allow us to dissect communities and ecosystems in a manner analogous to analysis of variance. R.A. Fisher recognized the importance of experimental design, and he provided the sword – analysis of variance – to slice nature up. Accordingly, we have the tools to analyse complex communities. The principle of reduction can be applied at the community level by dissecting a complex community into discrete multi-species assemblages, which are then differentially treated. By this method we can apply the statistical rigour of the null hypothesis at the community level.

> When factors are chosen for investigation, it is not because we anticipate that the laws of nature can be expressed with any particular simplicity in terms of these variables, but because they are variables which can be controlled or measured with comparative ease. The modifications possible ... must always be considered as potentially interacting with one another, and must be judged by the probable effects of such interactions. Indeed, ... an experimental investigation, at the same time as it is made more comprehensive, may also be made more efficient if by more efficient we mean that more knowledge and a higher degree of precision are obtainable by the same number of observations.[29]

Acknowledgements

We thank an anonymous reviewer for helpful comments on an early draft. This paper was partially supported by an NSERC operating grant to P. Keddy.

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