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MICROCOSM EXPERIMENTS HAVE LIMITED RELEVANCE FOR COMMUNITY AND ECOSYSTEM ECOLOGY[1]

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Introduction

Advantages of microcosm experiments are extolled by contributions to this Special Feature and other recent publications (Threlkeld 1993, Kareiva 1994). Some of my own work has benefitted from the speed, replicability, statistical power, and mechanistic insights attainable using microcosms, so I am not entirely opposed to the approach. Microcosms have become an important tool for some ecologists. However, microcosm experiments also have serious limitations. Without the context of appropriately scaled field studies, microcosm experiments become irrelevant and diversionary.

Why are ecologists tempted to build programs around microcosm experiments? In addition to the basic-science insights they provide, microcosms have other, more pragmatic advantages. Microcosms provide rapid results to meet publication goals for career development. Costs can be modest, so microcosm experiments are attractive for theses. Laboratory experiments keep ecologists on campus, where administrators would like them to be, instead of traveling to remote field sites. These advantages are important in the competition between environmental sciences and molecular biology that drives many biology departments.

[1] For reprints of this Special Feature, see footnote 1, p. 663.

Microcosms are easily justified to molecular colleagues in arguments for ecological appointments. But a molecular biologist who isolates ribosomes is working on ribosomes; an ecologist who isolates organisms in bottles may not be working on communities and ecosystems in any relevant sense. The approach works in molecular biology for a number of reasons: there is general agreement about the human health goals that rationalize most of the funding; statistical issues are few and often simple; the scientific community focuses on only a few species; and relatively rapid replicated study is possible at several levels (including organisms, the ultimate context for the science), so context is readily retained. These features are not shared by community and ecosystem ecology. Emulation of molecular biology by ecologists is "cargo-cult science" (Feynman 1985:308–317) with a serious cost: loss of relevance.

Ecological Experiments are Possible at Many Scales

Ecological systems do not have a single characteristic scale. Insightful research is likely to consider a range of different scales, including microcosms (Levin 1992). But in comparing results across scales, one must consider the extent to which microcosms represent ecological phenomena. The size and duration of microcosm experiments exclude or distort important features of communities and ecosystems. Some processes and organisms are too large, wide ranging, or slow to include in microcosm experiments. Examples are turbulence, migration, wolves, salmon, and trees. Other processes and organisms change so rapidly that they can reach unrealistic rates or population densities in the course of microcosm experiments. Examples are microbial metabolism, nutrient regeneration, phytoplankton production, bacterial biomass, and plankton communities.

Limnology provides many examples of disconnection between microcosms and natural systems. Container size and experimental duration are known to affect results (Gerhart and Likens 1975, Stephenson et al. 1984, Bloesch et al.1988). In one study, increases or decreases by phytoplankton during whole-lake grazer manipulations were correctly predicted for only a third of the taxa tested in microcosm experiments (Carpenter and Kitchell 1988). During the eutrophication controversy of the 1960s and 1970s, microcosm experiments caused the significance of inorganic carbon limitation in eutrophication to be overstated (Schindler et al. 1972). Phosphorus control policies were delayed until whole-lake experiments, comparative studies, and case studies showed convincingly that phosphorus loading caused eutrophication (Vollenweider 1976, Schindler 1977, Edmondson 1991). Currently there is controversy about the interactions of phosphorus loading and food web structure in controlling phytoplankton. Fish predation and phosphorus cycling occur at whole-lake scales and are difficult to mimic in microcosms. A recent review found confusion and contradiction among 44 studies; 22 of these were experimental but only four experiments were conducted at the scale of lakes (DeMelo et al. 1992:tables 2 and 3). The logical conclusion is that microcosms and non-manipulative studies have not yielded consistent results, and whole-lake manipulations are rare. The scale of research now emphasizes deliberate manipulations of whole ecosystems (Benndorf 1990, McQueen 1990, Carpenter and Kitchell 1993, Scheffer et al. 1993, Reynolds 1994).

These aquatic examples primarily illustrate problems of inappropriate spatial scale. Analogous problems occur when duration of experiments is too short. Overly brief experiments have proven misleading because of failures to account for transient dynamics, indirect effects, environmental variability, multiple stable equilibria, and site history (Tilman 1989).

Examples of experiments that were eventually recognized as misleading can be cited for many fields, at many scales. Microcosms are not the only research tool susceptible to misinterpretation. But microcosms are a very indirect way of learning about ecology, and there is considerable risk of results that are misleading about natural processes at relevant scales. Studies of appropriate scale and duration provide crucial checks for reliability of microcosm results.

Can we predict where microcosm experiments are likely to be useful? Successful microcosm experiments are prompted and verified by results of larger field programs (Frost et al. 1988). Typical case studies of large, unique ecological systems synthesize evidence from a variety of sources and approaches, which can include microcosms (Shrader-Frechette and McCoy 1993). For example, microcosms can be used to eliminate hypothesized mechanisms, compare alternative mechanisms, or estimate rates. Context and relevance, however, derive from appropriately scaled field studies.

Fortunately, experimental scales can be broadened in space and extended in time to include large, slow phenomena (Likens 1985, Tilman 1989, Levin 1992). Large-scale, long-term experiments can yield informative contrasts that test hypotheses and quantify effects at multiple scales simultaneously (Carpenter 1988). Statistical issues in the design of large-scale experiments require careful consideration; this active area of research is beyond the scope of this paper (but see Stewart-Oaten et al. 1986, 1992, Walters 1986, Carpenter 1988, 1990, Walters and Holling 1990, McAllister and Peterman 1992, Carpenter and Kitchell 1993, Scheiner and Gurevitch 1993). Inference in large-scale field studies depends on long-term databases (Likens

1989, Risser 1991), cross-system comparisons (Cole et al. 1991), and big manipulations (Likens 1985, Walters 1986, Carpenter 1990, Lee 1993). Such long-term and spatially extensive studies establish the context for ecological science. Misleading inferences are greatly reduced by scaling research tools to the spatial and temporal extent of ecological processes.

Scales of Environmental Problem Solving

Ecology has become a significant applied science with a responsibility to the society that supports it (Likens 1992, Lee 1993, Shrader-Frechette and McCoy 1993). The contribution of ecology to environmental problem solving depends heavily on appropriately scaled field studies. Examples of relevant scales are species ranges in conservation biology, watersheds in ecosystem studies, and global cycles in biogeochemistry. Academic ecologists may avoid these scales in order to attain the rigorous experimental control possible in microcosms. However, great benefits can arise when academic ecologists become involved in applied studies at relevant scales. Many innovations and insights necessary for effective work at the scale of management have come, and must continue to come, from academia. As noted in a recent evaluation of a partnership between a university and a management agency (Kitchell 1992:543), "Academics have the freedom to have lots of ideas. Being around and involved when these are developing can yield tremendous benefits." Basic ecology benefits also, as applied problems stimulate new questions in the same way that clinical issues motivate biomedical research (Slobodkin 1988).

Most of the crucial questions of applied ecology are not open to attack by microcosms (Carpenter 1988, Lee 1993, Shrader-Frechette and McCoy 1993). Tests of fish management policies (Hilborn 1992, McAllister and Peterman 1992), biomanipulation (Kitchell 1992, Carpenter and Kitchell 1993), and ecosystem management of the Columbia River watershed (Lee 1993) are a few examples. Field studies at the scale of the environmental problem are essential when phenomena of interest cannot be bottled (Carpenter 1988, Lee 1993) and when managers or stakeholders are not convinced by small-scale trials (Carpenter and Kitchell 1992, Lee 1993). The statistical advantages of microcosms (obtained through replication and ease of repetition) do not offset the problems of scale. In management, a 50:50 chance of success can be more persuasive (relative to alternative options with higher risk) than scientific certainty at the arbitrary 95% level (Walters 1986, Lee 1993). Decision makers may not have time to delay until statistical significance is high, because resources and political opportunities will disappear while they wait (Lee 1993). Learning by doing is a hallmark of successful environmental management (Holling 1978, Walters and Holling 1991, Lee 1993).

A Feeling for the Ecosystem

Who will train the ecologists needed for field science? It is irresponsible for academic ecology to produce larval microcosmologists by canalizing graduate students into careers of small-scale experimentation. There is cognitive danger that the microcosm (rather than the ecological system) will become the object of study, leading to needless confusion as results are overinterpreted and overextended. As ecology becomes more and more a science done indoors by urbanites, there is significant risk of losing our sense of context. Already there is a shortage of students and postdoctoral students who have the practical knowledge and natural-history background to function outdoors. Graduate curricula in ecology could fill gaps in practical knowledge through courses in hardware, lumberyards, construction, boat and motor maintenance, field methods, and so forth. But graduates who lack a deep appreciation of natural history and real ecosystems, which can come from extensive field experience but not from the campus, have deficient educations. Without the training environment provided by field research, there is likely to be a shortage of scientists capable of mounting insightful field programs.Those of us in academia should work to fill that need.

The rich context of ecology, our fundamental understanding of phenomena at multiple scales, and the significance of ecology to society depend on appropriately scaled field studies. While microcosm experiments have many advantages, their primary role is supportive and heuristic. Ecologists should use all available tools to advance the analysis of communities and ecosystems at the scales of natural processes, management, and societal concern.

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