

# Constructing Nature: Laboratory Models as Necessary Tools for Investigating Complex Ecological Communities

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I. Time, Scale, and Observation in Ecological Systems . . . . .	335
II. Contingent Structure and Reciprocal Interactions . . . . .	342
A. Historical Contingency and Ecological Processes . . . . .	342
B. The Interaction of Ecological Processes Operating at Different Spatial Scales . . . . .	344
C. What These Examples Tell Us . . . . .	345
III. Problematic Field Studies . . . . .	345
IV. The Role of Microcosms in Community Ecology . . . . .	346
V. Endnote . . . . .	349
References . . . . .	349

Ecological systems are arguably among the most complex of all systems found in nature at any scale of observation. The origin of this complexity arises not only from the stunning diversity of entities that comprise such systems (i.e., species, individuals and highly variable nature of interactions among these entities), but also because such systems exhibit non-equilibrium, non-linear, historically contingent, self-organizing behavior replete with a host of emergent properties and attendant noise. There are few constants or laws past thermodynamic constraints and simple mechanics, and here process and mechanism operate across vast scales of existence in a fashion that is not precisely replicable. The basic approach of ecologists has been brute-force observation and experimentation in specific settings, with the tacit hope that answers will emerge from large data collection. Laboratory experiments, of course, suffer from many of the same difficulties that plague field studies. At the same time, the simplifying assumptions of laboratory community studies permit explorations of intact communities—something never accomplished in the field (Drake *et al.*, 1996). But the lab is not enough. The general dynamic behaviors and phenomena observed in the lab provide fodder (in the form of potential and probable processes directing community structure) for field approaches.

Early explorations into the structure of ecological reality were largely limited to description and dominated by natural historians, typified by the supposedly inductive methodologies of the great Victorian naturalists, such as Richard Owen and Charles Darwin. This, of course, was the essential first step, as one must know what building blocks exist before any consideration of composite structure can be envisioned. Nevertheless, brilliant insights into possible inner-workings of ecological systems, by largely non-inductive methods, began to emerge in the late 1800s (e.g., Camerano, 1880; Forbes, 1887), and coupled with mathematical application (e.g., Volterra, 1926; D'Ancona, 1954) rapid progress was made in establishing working foundations for understanding nature.

Concomitant with this foundation, a variety of laboratory studies were conducted as tests of emerging paradigms in this loose discipline (Gause, 1934; Park, 1962). Early in the development of ecology as a science, investigators realized that the experimental use of rapidly growing species in a precisely controlled and readily replicated environment was essential to answering many of the questions posed by theory (Lawton, 1998; Jessup *et al.*, 2004). Literally thousands of generations can be readily observed and tracked in the laboratory using appropriate organisms; a thousand generations of birds, on the other hand, would require many generations of scientists devoting their entire lives to this single endeavor. However, there are a few examples of data collection and analyses selflessly extending beyond a single research career (e.g., Schindler *et al.*, 2003). Interestingly, and in similar fashion to the physical sciences, scientists working in the laboratory, in the field, and with models, fight among themselves for primacy (Kohler, 2002).

Here, we argue that laboratory studies are not only valid investigative tools, but may also better capture the essential dynamics of ecological systems compared with field studies. Through exploring the use of microcosms we wish to illustrate the dynamic reality of ecological systems and examine the systems in which explicit tests of these realities are possible. Further, we argue that most field studies, while remaining the cornerstone of ecology, are inadequate to answer many fundamental ecological questions largely because of inappropriate time series, field-induced reductionism, and unwieldy scale issues (Lawler, 1998). Such studies provide little more than a snapshot of ecological reality, exposing day-to-day variance and uncovering proximate mechanism. Herein lies the dilemma; laboratory studies are artificial constructs and caricatures of reality (where parameters are imposed by the would-be observer), while field studies address the real world but with little hope of stepping past the workings of the presently observed state. We offer that rather than being antagonistic approaches, as is the current state, field and laboratory studies should be conducted in concert. Field and

laboratory studies are inevitably linked by the ecological processes that bind all living organisms. However, insights into the workings of nature not only advance through direct observation but also through deductive and logical musings into ecological possibilities. Mathematical and conceptual models, we posit, make assumptions and predictions better tested, in the first instance, using controlled laboratory studies. For example, Tilman (1977) famously used algae in aquatic microcosms to test the predictions made by resource competition models (e.g.,  $R^*$ ). These concepts extended to and refined by natural grasslands provide validation of the power of a synergistic laboratory and field approach.

We proceed by examining various concepts in community ecology, which may be difficult to observe in natural systems and examine some laboratory studies that document the production of ecological structure in multi-species systems. Specifically, we will explore two aspects of ecology where laboratory studies are crucial for our understanding of ecological phenomena. The first aspect is parameter- and measurement-oriented, what must be measured and how should it be done to make observations in ecological studies. We ask whether we are adequately testing ecological theory. Secondly, we explore the interactive nature of ecological phenomena and our inability to reduce these processes to their constituent components. These two discussions implicitly address the relationship between reductionism and holism. Based on these, we will contrast the laboratory approach with the field and model approaches to identify the prescriptive role for laboratory microcosms in ecological research.

## I. TIME, SCALE, AND OBSERVATION IN ECOLOGICAL SYSTEMS

"Ecology differs from other natural sciences in its emphasis on the primacy of direct observation" (Keller and Golley, 2000, pg. 10). Given this, ecologists must be critical of what they are observing and what these observations mean, especially as they pertain to understanding nature. Nature viewed through human eyes is just that—reality tuned and created by a particular neural net and observed at specific long wavelengths, while being framed by mental limitations and preconceived ideas about what should be observed. Ecologists employ both empirical and theoretical models to formalize the operation of nature. Properly employed empirical and theoretical models feed back to one another, generating a worldview. For reciprocal translation between empirical and theoretical claims, models and observations have to be temporally and phenomenologically equivalent (Hastings, 2004) or we will enter the domain of the canonical apple- and-orange metaphor. There is

no need to invoke the age-old perceived tension between empiricism and rationalism, where 5th century BC contradictory philosophies of Heraclitus and Parmenides on the nature of change brought into question the reliability of observation (Lindberg, 1992). Instead, in ecology the ground seems ripe for a reciprocal relationship between the various methods of asking questions and obtaining knowledge about how nature works.

Ecological communities are composed of a vast array of variously interacting species, so much so that community investigations in the real world typically focus on something other than the community—generally, the set of visually prominent or taxonomically interesting species in some area (e.g., fishes, birds, invertebrates, lizards, trees and so on). We have argued elsewhere that erroneous conclusions about the nature of the community, and certainly its operation, are a necessary outcome of considering pieces of a larger structure (Drake *et al.*, 1996; Samuels and Drake, 1997). Just as the façade of a building reveals little of the internal structure capable of supporting that façade, analyses of pieces of communities have also led us astray and unfortunately such analyses form much of the present ecological paradigm. Herein lies one of the pre-eminent roles for laboratory experimentation—the ability to consider an intact and readily replicable ensemble of species. With microcosms, ecologists have the ability to construct communities as complex or simple as desired. In these systems, species composition, trophic structure and complexity are readily manipulated (e.g., Balčiūnas and Lawler, 1995). For example, Fox and McGrady-Steed (2002) examined the role community complexity plays in system-level properties such as ‘stability’. Several recent microcosm experiments attempted to account for all species at all trophic levels within the system, from bacteria to top predators (e.g., Balčiūnas and Lawler, 1995; Morin, 1999; Diehl and Feiße, 2000; Fox 2002) or even manipulate multiple trophic levels (e.g., Naeem *et al.*, 1994), in order to better understand the role various phenomena play in community dynamics. Without doubt, powerful analyses such as these are all but impossible in the ‘real world’. However, armed with concepts, dynamics and behaviors observed in the lab, the pieces of nature, which are intractable in the field, may yield their secrets.

Approaching the appropriate structure, however, is only one aspect of an adequate community characterization. These are generally long-lived structures where dynamics on a successional time scale must be invoked to understand observation. Even at simpler levels of organization, multigenerational data often reveal aspects of population dynamics not readily observed in short studies. In examining population dynamics of weedy annual plants, Freckleton and Watkinson (2002) noted that long-term data were required and that such data were surprisingly rare. When we start looking at basic interspecific interactions, the number of generations of competitors or predators and prey required to expose the essential dynamic nature of these

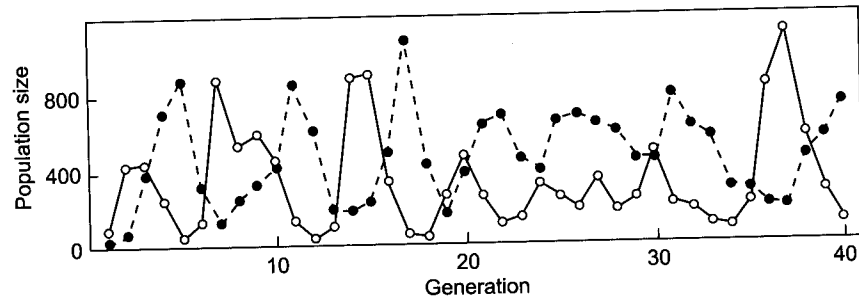
interactions can be enormous (Table 1). Tilman's (1977) elegant studies of competition between diatoms employed the highly controllable environment of the chemostat. Given the duration of the study and organisms involved, Tilman likely observed somewhere between 15 and 30 generations before dynamics were definable. Similarly, Gause's (1934) paramount competition studies with protists spanned roughly 20 generations. Other relatively ‘simple’ experiments (Table 1) still required multiple generations to show relevant patterns. Luckinbill (1973) and Vandermeer (1969) both examined two-species dynamics (predator-prey in the former and competition in the later), and both required at least 10 generations to correctly parameterize dynamics. More recently, Holyoak and Lawler (1996) examined a two-species, predator-prey metapopulation and due to the complicating factor of habitat subdivision, they needed at least 25 generations to observe cyclic population dynamics. Similarly, Morin (1999) needed at least 50 generations to observe outcomes of two-species competition experiments.

Utida (1957) presented laboratory time-series data of a host-parasite system. The first five generations of his study show a crash in the parasite and an increase and subsequent crash in the host (Fig. 1). This length of time is readily scalable to, for example, five years worth of breeding bird data. However, the oscillatory nature of this interaction does not become apparent for at least 10 generations, and an observable damping of oscillations did not occur for at least 25 generations (Fig. 1) (Utida, 1957). Utida's (1957) experiment reveals that observations at three different temporal scales could potentially lead to three different conclusions about host-parasitoid dynamics. The need for long-term observations also seemed to strike Utida, when commenting on a paper he previously published on the same data. “This trend of convergence was not found in the data described in the previous paper, for the 25 generations provided too short a time in which to detect it” (Utida, 1957, pg. 443). Relatively long time series are necessary to establish the dynamic nature of a single mechanism, under highly controlled conditions.

However, do Utida's findings typify other systems? What about characterizing complex population dynamics, where the stochastic process potentially lead to apparently chaotic trajectories? The relatively few instances where long-term field data have been collected seems to largely support the notion that population dynamics are often non-linear (Kendall, 2002). In order to properly characterize non-linear dynamics in field populations, data spanning decades is required. Unfortunately, these types of data are rare (Freckleton and Watkinson, 2002). Even less common are situations where long-term demographic data are collected on more than one interacting species, and yet this type of data are regarded as quintessential for understanding non-linear dynamics (e.g., Krebs *et al.*, 1995; King and Schaffer, 2001). The idea of non-equilibrium, transient ecological systems has changed

Table 1 Examples of multispecies microcosm studies of ecological phenomena

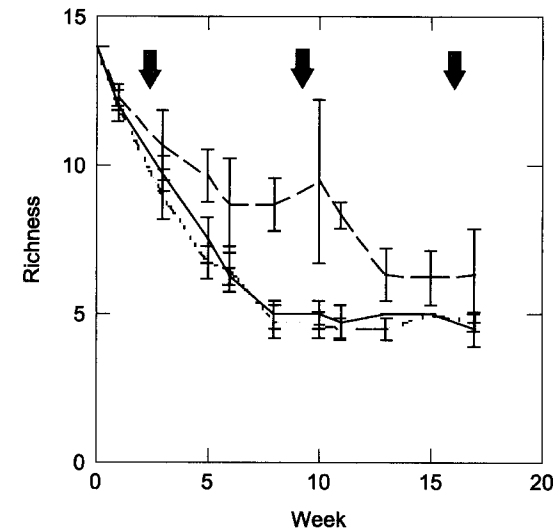
Researchers	Organisms	Ecological phenomena	Time scale of result
Balčiunas and Lawler, 1995	Two ciliate prey and a single predator	Resource level, predation and prey composition on dynamics	Experiment ended on day 50 (50 or more generations of species) and some results not finalized (e.g., their Fig. 4—not clear if cyclic or extinction, and Fig. 5a—extinction trajectory?)
Dickerson and Robinson, 1985	19 species of algae, protists and rotifers	Richness-area relationships	About 20 weeks (more than 100 generations) needed for patterns
Diehl and Feibel, 2000	Bacterial basal level and ciliate consumer and omnivore	Resource level on three-level food chains with omnivory	Outcomes of experiments were not realized, in some cases, until 100 to 150 generations into the experiment
Drake, 1991	13 species of algae, protists, cladocerans and amphipods	Assembly sequence and community structure	Systems still dynamic from 60 to 160 days
Have, 1993	Two rotifers, one Ostracoda and 20 ciliates	Species-area relationships	Species-area relationships continue to change up to 90 days (i.e., 90 generations for most species)
Holyoak and Lawler, 1996	Single predator and prey pair	Predator and prey population dynamics across patchy landscape	At least 25 generations to see nature of cycles
Lawler, 1993	Two ciliate bacteriovores, one intermediate predator and top predator	Multi-trophic interactions and population dynamics	At least 50 generations for four species treatment
Lawler and Morin, 1993	Two bacteriovorous and one omnivorous ciliates and two Sarcodine predators	Food-web architecture and population dynamics	Depending on composition, up to 40 days needed (i.e., about 40 generations)
Luckinbill, 1973	Ciliate predator and prey	Predator-prey co-existence	At least 15 days generations to observe two full predator-prey oscillations
McCauley and Murdoch, 1990	Daphnia and algae	Resource and predator-prey dynamics	200 days to observe cycles
McGrady-Steed <i>et al.</i> , 1997	Algae, herbivore rotifers and protists and predators	Biodiversity and ecosystem predictability	Diversity stabilized at about 24 generations
Morin, 1999	Bacteria and two ciliate bacteriovores	Competition dynamics at differing resource concentrations	Two-species competition dynamics continued to change after 50 days
Petchey, 2000	Three ciliate bacteriovores and single predator	Community complexity and stability	Equilibrium around 16 generations
Robinson and Edgemon, 1989	28 species of algae and protists	Predation and invasibility of communities	Equilibrium after 15 weeks (about 100 generations)
Tilman, 1977	Two species of algae	Resource competition	Some cases more than 20 generations required
Utida, 1957	Bean weevil larvae and parasites	Host-parasite dynamics	10 to 25 generations to observe nature of cyclic patterns
Vandermeer, 1969	Three ciliates	Ciliate competition	Single populations took about 10 generations to reach carrying capacity
Weatherby <i>et al.</i> , 1998	63 combinations of six protists species	Persistent communities	Community persistence could not be assessed until 10 to 100 generations of constituent species



**Figure 1** Fluctuations in population size in azuki bean weevil, *Callosobruchus chinensis* (open circles), and its larval parasite, *Neocatolaccus mamezophagus* (closed circles). Adapted from Utida (1957).

how we conceive of ecological dynamics (Hastings, 2004). However, laboratory studies offer the ability to manipulate parameters and test predictions about the nature of non-linear dynamics (Constantino *et al.*, 1995, 1997). Constantino *et al.* (1997) famously used *Tribolium* beetle laboratory populations to test mathematical theory predicting population transitions to chaotic dynamics. By manipulating mortality and recruitment rates they were able to predict when population dynamics changed from stable equilibrium to quasiperiodic cycles to chaos. To do a manipulative field experiment like that of Constantino *et al.* (1997), which integrates predictive models with real data would require decades of labor and vigilance. Probably the most famous case of data showing non-linear dynamics in natural populations (lynx-hare dynamics) (Krebs *et al.*, 1995) was a serendipitous study, via hunting records. Although immensely valuable and insightful, such a time series does not represent the rigorous methodology that is expected of modern experimental ecology.

The aforementioned examples examined ecological phenomena associated with relatively 'simple' situations with a few species, and yet required truly multigenerational observations. However, community ecology is often concerned with much more complex assemblages, where multiple processes may be interacting to produce the observed patterns. Such complex assemblages likely require even longer observational time series in order to adequately account for community dynamics. For example, Cadotte and Fukami (2005) needed from 50 to 100 generations of the organisms making up microcosm communities to adequately observe richness patterns in groups of communities (Fig. 2). In their experiment, they observed patterns of species richness at the metacommunity level, where the different treatments corresponded to differing levels of dispersal. From Fig. 2, it is readily apparent that although initial conditions were identical, one of the treatments (no dispersal) showed a different history compared to the other two



**Figure 2** Change in landscape-level richness over time in three dispersal treatments (dashed line refers to no dispersal treatment). Adapted from Cadotte and Fukami (in review). The three arrows, discussed in text, refer to the fact that differing conclusions would be drawn if the system were sampled at these time periods.

treatments, despite the fact that the metacommunities end up at similar richness states. Singular observations at the three arrows would lead investigators to different conclusions about the role of dispersal.

In general, studies employing more complex community structures required many generations (usually 50 or more) to adequately account for community dynamics (Table 1). Microcosm studies investigating species-area relationships (Dickerson and Robinson, 1985; Have, 1993) required many generations (at least 90) to account for these patterns. In fact, Have (1993) showed that the nature of the species-area relationship quantitatively changed up to 90 days into the experiment, when the experiment was terminated. Studies examining the effect of resource level on species interactions (McCauley and Murdoch, 1990; Balčiunas and Lawler, 1995; Diehl and FeiBel, 2000) all required more than 50 generations to make adequate observations. Invasion resistance is another concept where microcosms offer great opportunity in advancing our understanding. Robinson and Edgemon (1989) used 28 species of algae and protozoan to investigate invasion resistance, they needed about 100 generations to address invasion resistance in communities. Assembly history is an area of investigation in community ecology which can only be sufficiently addressed by microcosm studies (see more on this in section II.A). Drake (1991) investigated the process of

community assembly on community structure and made observations for 60 to 160 days, where most of the organisms he used had a generation time of about a day. Several other studies, examining such things as food-web interactions and population dynamics (Lawler, 1993; Lawler and Morin, 1993; Diehl and Feißel, 2000), needed anywhere from 40 to 150 generations to observe crucial dynamics. Many of these studies reveal that there may be no *a priori* determination of the number of generations needed to make sufficient observations. A number of these results observed changes in dynamics or patterns at some later time in the experiment. Time-specific observations (such as at the arrows on Fig. 2), depending on the hypotheses being tested, would seriously restrict inferential space and possibly lead to erroneous conclusions. Perhaps even worse is the contention that the origins of observed dynamics require even more historical information that is unavailable by direct experimentation (Drake *et al.*, 1999). We are not suggesting that microbial systems are any less prone to exhibiting transient patterns after many generations, but that if transient behavior typifies natural systems (Hastings, 2004), we had better be able to observe them.

## II. CONTINGENT STRUCTURE AND RECIPROCAL INTERACTIONS

Laboratory studies can address fundamental questions. Here we address two rapidly expanding foci of study in ecology: the interaction between historical contingency and ecological processes, and the interaction among processes operating at different spatial scales. The processes constituting these two foci do not appear to be understandable in terms of dichotomous states, which are often the typology used to conceptualize or parameterize ecological systems (Peters, 1991). Nor are these properties likely to be reducible to constituent components (e.g., Levins and Lewontin, 1985). The role for microcosms in examining intertwined and possibly non-reducible processes is enormous. Despite the fact that very sophisticated statistical models have been developed to tease apart avenues of causation in ecological systems [e.g., path analysis (Shiple, 2000)], field studies likely lack the temporal scale and manipulative control to investigate the nature of such processes.

### A. Historical Contingency and Ecological Processes

There is no doubt that both historical contingency and local ecological dynamics are paramount processes in shaping communities. From an early point in time, interspecific interactions, such as competitive exclusion and

predation, have been recognized as key factors in community dynamics (e.g., Gause, 1934; Huffaker, 1958; Chase and Leibold, 2003). More recently, understanding the contingent nature of community assembly has also been considered necessary for understanding community patterns (e.g., Drake, 1991; Drake *et al.*, 1999; Law and Morton, 1996). These two community-structuring influences (interspecific interactions and community assembly) are not readily separable, and understanding this interaction requires highly controlled and replicable experiments. We say that they are not readily separable because, although we can conceptualize a community where all possible species from the regional pool arrive at the same time (the community inception) and hence interspecific interactions are the primary structuring process, this is very unlikely to be the case in most systems. Therefore, most communities must have some history of assembly or continuing invasion where the arrival of a novel species initiates new sets of interspecific interactions (such as in community succession). The lack of independence stems from the idea that each arriving species, if it persists, interacts and changes some portion of the community into which it invades.

Two recent studies suffice to show the importance of the interactive nature of history and local processes. First, Warren *et al.* (2003) showed that, what they termed 'catalytic species', could not persist in either of two possible final community states, but yet switch the communities between these two states via their invasion. One of the two end communities could not be reassembled from the final species membership (aka Humpty-Dumpty community) (e.g., Luh and Pimm, 1993; Samuels and Drake, 1997), but required the presence of the catalytic species in the community's assembly history. Although the final communities appear to be structured by local interactions, assembly history appears to have a critical role in directing structure to alternative basins of attraction. The two antithetical models of community assembly—deterministic versus alternative stable states—appears to actually not be dichotomous but co-occurring processes.

A second recent study, by Fukami and Morin (2003), showed that productivity-diversity relationships, which are often thought to be caused by local dynamics, may depend upon the history of community assembly. They show that productivity-diversity relationships are greatly influenced by assembly history of protozoan invasions into microcosm communities. Previous to this study, Waide *et al.* (1999) summarized research into productivity-diversity patterns, and found that a number of different patterns are commonly found in nature. Fukami and Morin (2003) showed that depending on assembly sequence, linear, quadratic (convex and concave), and non-significant productivity-diversity patterns were all possible. This research reveals that community assembly processes may be very important for understanding extant ecological patterns.

## B. The Interaction of Ecological Processes Operating at Different Spatial Scales

There have been a number of recent theoretical studies examining species co-existence as the product of ecological processes operating over larger spatial scales (e.g., Amarasekare and Nisbet, 2001; Shurin and Allen, 2001; Mouquet and Loreau, 2002). Early work by Horn and MacArthur (1972) and Levin (1974) showed that competitively inferior species could co-exist with competitively superior species given a spatial context. The mechanism for this co-existence is a colonization-competition tradeoff, where competitively inferior species are likely to be superior at colonizing new habitats. Since that time the idea that local-level processes (e.g., competition and predation) and larger-scale processes (i.e., dispersal) are important for shaping biodiversity patterns has been formalized (e.g., Srivastava, 1999). Community ecology research concerned with patterns at larger spatial scales, involving multiple local communities, is referred to as the metacommunity-level (more detail on the metacommunity will be discussed in the following text).

A number of studies view the effects of local and regional processes as discrete and in some cases as diametrically opposing forces. These processes may not be readily separable, in similar fashion to the interaction between historical contingency and local processes previously mentioned. Dispersal of propagules originates from within patches, which is likely related to the density of individuals. At the same time, dispersal of new individuals into a habitat likely alters local population dynamics and species interactions thereby revealing the integrated nature of these two processes (e.g., Levins and Lewontin, 1985). The research into the interaction between local and regional processes has not kept pace with theoretical advances. However, some recent work, utilizing both laboratory and field microcosms, have addressed the influence that dispersal has on structuring local communities and diversity patterns (Warren, 1996; Shurin, 2001; Kneitel and Miller, 2003). Important advances in this area have been made by Marcel Holyoak and colleagues who examined metapopulation dynamics of interacting species (e.g., Holyoak and Lawler, 1996; Amezcuca and Holyoak, 2000; Holyoak, 2000). Although the role of dispersal on more complex assemblages is only just beginning, one of the greatest strengths of microcosms is the ability to control and quantify dispersal. Quantifying dispersal has been an incredible challenge in natural systems, and it is essential for testing models.

A frontier of modern community ecology is examining the processes and dynamics occurring at spatial scales larger than the local communities, and vast potential rests in this area of research (e.g., Maurer, 1999). This recent area of research has greatly benefited from advances made by microcosm experiments done both indoors and outdoors (Warren, 1996; Shurin, 2000, 2001; Kneitel and Miller, 2003; Cadotte and Fukami, 2005). We would

define the metacommunity as not just immigration and emigration of individuals among local communities—which is important—but also the interconnectedness of community processes. This interconnectedness arises via the moving of competitive and predatory interactions, stabilizing and destabilizing units, chaotic attractors and so on among local communities. If local communities exhibit local chaotic attractors directing community patterns, then what happens when these local systems are interconnected? Do local attractors themselves converge, or do we get some higher-level, emergent phenomena at the metacommunity scale? These complex issues, in the immediacy, can only be addressed using highly controlled microcosm systems, where again, the proper time scales are crucial.

## C. What These Examples Tell Us

These two examples of complex interrelations of ecological processes are not meant to convey the perception that microcosms can reduce ecological phenomena to their constituent processes. Rather, laboratory microcosms offer an important avenue towards observing and measuring these interactive, intertwined processes and emergent properties. In the first case (contingent history), Fukami and Morin (2003) reveal that local processes do create a productivity-diversity relationship, but the exact nature of these relationships is highly influenced by history. All natural communities have history. Understanding the influences of history requires ecologists to follow communities from their inception through many generations, something that few field systems would allow (Berlow, 1997; using sessile marine organisms is a notable exception). In the second example (processes at different spatial scales), microcosm studies are crucial because researchers can examine communities structured only by local processes and compare them to communities that include regional dynamics. Microcosms allow controlled experiments to understand how local and regional processes combine to structure local communities.

## III. PROBLEMATIC FIELD STUDIES

Some questions in ecology are of fundamental importance, given the current expectations for ecologists to predict the consequences of human-caused environmental impacts (Lawton, 2000; Shrader-Frechette, 2001; Ehrlich, 2002). The importance of these questions are confounded by the ethical dilemmas of performing experiments on intact communities, or the fact that constructing and replicating human-caused change may be functionally impossible to engineer. Microcosms offer much to the field of invasion biology. Whereas there are obvious ethical concerns about purposefully introducing invaders into intact

systems, as well as manipulating parameters such as richness of these intact communities, microcosms are able to overcome these ethical concerns (e.g., Robinson and Edgemon, 1989; McGrady-Steed *et al.*, 1997).

Similarly, the effects of global change are of great concern for many ecologists. Yet, answering the question of how global change may affect communities is very complex, and the experiments (including FACE sites) are expensive and, due to small sample sizes, statistically cumbersome. Microcosm investigations into global change (Petchey *et al.*, 1999) not only can overcome many logistical problems, but also could be used to inform what factors field studies should look at.

#### IV. THE ROLE OF MICROCOSMS IN COMMUNITY ECOLOGY

Gilpin *et al.* (1986) noted that laboratory microcosm experiments have a great potential to offer insight into ecological communities, but that lab experiments thus far were too simplistic. In the almost 20 years since the Gilpin *et al.* (1986) paper, there have been several important studies into the structure of communities using microcosms. Examples include: Drake (1991); Lawler (1993); Diehl and Feiel (2000); Holyoak (e.g., 2000); Fox and McGrady-Steed (2002); and most recently Warren *et al.* (2003). Present microcosm studies are examining much more complex assemblages and phenomena compared with earlier studies.

There is concern that energies devoted to laboratory studies may be better spent for advancing theoretical models, since laboratory microcosms are essentially messy models. This concern misses the many potential contributions, stark and subtle, that laboratory research offers (e.g., Lawton, 2000; Jessup *et al.*, 2004). True, laboratory systems are much simpler than real ones and use organisms which are themselves physically and behaviorally simpler than other organisms and, in a sense, follow many simplifying assumptions in general models (e.g., asexual reproduction, discrete community borders, stable trophic structure and so on). Gilpin *et al.* (1986) rightly noted that future lab studies would find that laboratory communities have inherent complexity. This complexity is at the heart of why laboratory communities are so useful to ecologists. This complexity indicates that assemblages of species may exhibit patterns that are on the one hand greater than the sum of their parts, and on the other may reveal patterns and dynamics not predicted by mathematical models (see more discussion in the following text on variability and stochasticity in microcosms).

One of the greatest strengths of microcosm systems is the ability to directly test theoretical models. Examples include Constantino *et al.* (1995, 1997) and Warren *et al.* (2003), both previously discussed, as well as experiments

comparing predictive models of predator-prey interactions (Bohannon and Lenski, 1997; Kaunzinger and Morin, 1998). Experimental microcosms also refine theory by stipulating under what circumstances processes operate. For example, experimental microcosms show that the intermediate disturbance hypothesis operates as the well-known unimodal relationship in heterogeneous environments but as a linearly declining relationship in homogeneous environments (Buckling *et al.*, 2000).

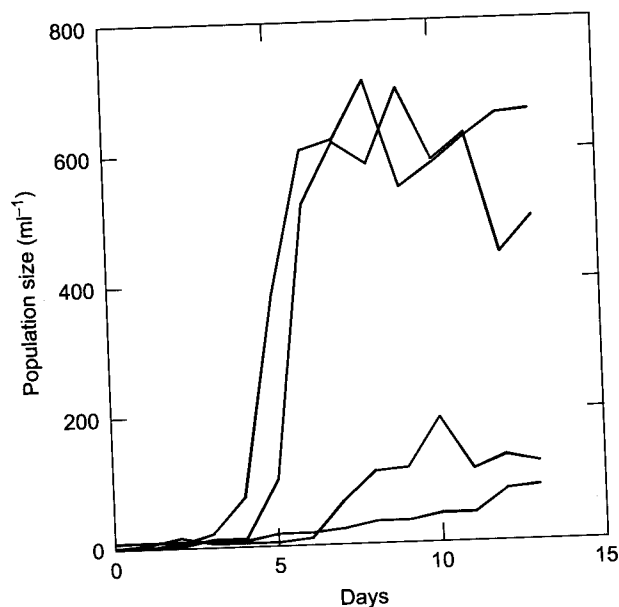
Diamond (1986) rightly notes the important contributions that microcosm studies have had on fundamental principles of ecology. However, we disagree with his assessment that lab experiments are weak in terms of temporal and spatial extrapolations. A most recent reincarnation of the same idea can be found in the otherwise excellent article by Ricklefs (2004, p. 5). Their conceptualization of temporal scale seems to rest on 'real' time (measured in days), where laboratory studies typically run for less than one year. However, different organisms should be viewed under the auspices of generational time (Petersen and Hastings, 2001). As previously discussed, laboratory experiments may follow populations for many more generations than in many field studies. Diamond believes that "[natural experiments] are the sole method capable of studying the genetic changes after 10,000 years." Yet work by Lenski *et al.* (2003) on genetic changes over tens of thousands of generations in bacterial populations reveal immense insight into what laboratory experiments offer. This is not to say that bacterial population dynamics offer particular insights into, for example, marine mammals, but our general understanding of genetic change and ecological factors has been greatly advanced by such microcosm studies (e.g., Bohannon and Lenski, 1997; Lythgoe and Chao, 2003; Yoshida *et al.*, 2003).

As for spatial scale, Diamond (1986) and Ricklefs (2004) seemed to compare scale to human relative measurements, while we would argue that spatial scale should be relative to the scale of ecological processes of the organisms involved. Again as previously outlined, laboratory experiments can include habitat heterogeneity and larger spatial processes. For example, Ricklefs's (2004) hypothesis that diversity patterns are historically contingent over large scales can be explicitly tested by laboratory microcosms in ways that are not otherwise possible (Rainey and Travisano, 1998; Fukami and Morin, 2003). More importantly, the criticism that microcosms are too simple and too small a scale ignores that, with care, systems can be scaled down with appropriate processes and dynamics being maintained (Petersen and Hastings, 2001).

An important criticism is that microcosms limit variability and stochasticity, which may be critical for real communities. Again, we believe that microcosm studies can help ecologists understand the potential roles variability and stochasticity play in ecological communities. Environmental variability can be not only eliminated, but also induced (e.g., Petchey *et al.*, 2002) to see how variability interacts with other processes. More

subtle is the role stochasticity plays in ecological processes. As noted earlier, laboratory systems can still exhibit chaotic fluctuations and exhibit stochastic and other complex or unexpected patterns. For example, the results of a recent experiment (Fig. 3; Cadotte, unpublished data, 2003) show that the inherent stochastic nature of population dynamics in monocultures of *Paramecium aurelia*. The four population trajectories correspond to identical initial conditions, and yet two of the four replicates reach a carrying capacity of about 600 individuals/ml in six days, while the other two replicates settle at <100 individuals/ml. These apparently stochastic processes may be the result of a number of mechanisms, from genotype differences to contamination of infectious agents or toxic microorganisms such as fungi. This is not to say that microcosms do not confer a high degree of repeatability (e.g., Holyoak and Lawler, 1996; Morin, 1999), but microcosm populations are not immune to uncontrolled stochasticity. Whereas natural systems may not allow ecologists to witness stochastic trajectories (rather, time-specific variation), microcosm communities allow ecologists to observe stochastic trajectories in controlled replicated experiments.

We see laboratory microcosms as the link between models and the real world. The reasons for this have been outlined throughout this chapter.



**Figure 3** Population growth curves for four populations of *Paramecium aurelia* in identical conditions, showing the stochastic nature of population growth (Cadotte, unpublished data).

Basically, we are forwarding the notion that there may be a discontinuity between general models and observations based in the real world. This continuity comes in the form of scale of observation (temporal and spatial), elucidating non-independent and contingent processes, as well as observing complex, unexpected patterns.

## V. ENDNOTE

Science advances by the generation of new theories, solving existing puzzles within the extant framework, and the largely non-epistemological need to explain more phenomena with fewer explanations. Scope, simplicity and fruitfulness are several measures of useful and growing research programmes (e.g., Brown, 2001), although we must also not forget the value of specificity in science (Motokawa, 1989; Simberloff, 2004). The ability to address important problems depends upon scientists being able to ask the correct questions and make precise and unequivocal observations.

In ecology, important problems abound. Field studies and conceptual models have helped ecologists clarify some of the critical problems, yet natural systems are teeming with complexity, so much so that there seem to be exceptions to any rule. Should we resign ourselves to accept that we may never be able to disentangle patterns in community ecology? Or that we may only be able to make generalizations at extreme macroscopic scales (Lawton, 1999)? We would argue that, in the face of insurmountable complexity, we redouble our efforts, using new tools and concepts, deconstruct and reconstruct communities and use our ability to construct functioning caricatures of nature in the laboratory. Microcosm communities are real communities, although not natural. They contain the same types of interacting species: competitors, predators and prey, mutualists and so on; undergo the same types of processes: species extinctions, succession, species sorting and so on; and show the same type of patterns: diversity-productivity patterns, community complexity and resultant stability, species-area relationships and so on. We argue then, given that microcosm communities confer experimental benefits, they are more useful for understanding some of the primary processes in community ecology than generally thought.

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