

# Are natural microcosms useful model systems for ecology?

Diane S. Srivastava<sup>1</sup>, Jurek Kolasa<sup>2</sup>, Jan Bengtsson<sup>3</sup>, Andrew Gonzalez<sup>4</sup>, Sharon P. Lawler<sup>5</sup>, Thomas E. Miller<sup>6</sup>, Pablo Munguia<sup>6</sup>, Tamara Romanuk<sup>7</sup>, David C. Schneider<sup>8</sup> and M. Kurtis Trzcinski<sup>9</sup>

<sup>1</sup>Department of Zoology and Biodiversity Research Centre, University of British Columbia, 6270 University Blvd, Vancouver, BC, Canada, V6T 1Z4

<sup>2</sup>Department of Biology, McMaster University, 1280 Main Street West, Hamilton, ON, Canada, L8S 4K1

<sup>3</sup>Department of Ecology & Crop Production Science, SLU, Box 7043, SE-750-07 Uppsala, Sweden

<sup>4</sup>Department of Biology, McGill University, 1205 ave Docteur Penfield, Montreal, QC, Canada, H3A 1B1

<sup>5</sup>Department of Entomology, University of California at Davis, Davis, CA 95616, USA

<sup>6</sup>Department of Biological Science, Florida State University, Tallahassee, FL 32306-1100, USA

<sup>7</sup>Département des Sciences Biologiques, Université du Québec à Montréal, CP 8888, Succ. Centre Ville, Montréal, QC, Canada, H3C 3P8

<sup>8</sup>Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF, Canada, A1C 5S7

<sup>9</sup>Department of Biology, Dalhousie University, Halifax, NS, Canada, B3H 4J1

**Several recent, high-impact ecological studies feature natural microcosms as tools for testing effects of fragmentation, metacommunity theory or links between biodiversity and ecosystem processes. These studies combine the microcosm advantages of small size, short generation times, contained structure and hierarchical spatial arrangement with advantages of field studies: natural environmental variance, 'openness' and realistic species combinations with shared evolutionary histories. This enables tests of theory pertaining to spatial and temporal dynamics, for example, the effects of neighboring communities on local diversity, or the effects of biodiversity on ecosystem function. Using examples, we comment on the position of natural microcosms in the roster of ecological research strategies and tools. We conclude that natural microcosms are as versatile as artificial microcosms, but as complex and biologically realistic as other natural systems. Research to date combined with inherent attributes of natural microcosms make them strong candidate model systems for ecology.**

Most disciplines in biology make extensive use of model systems. Ecology, by contrast, has only a few putative model systems (e.g. *Tribolium* beetles for population ecology, Darwin's finches for evolutionary ecology, and anurans in cattle tanks for community ecology). We believe that ecologists have not taken full advantage of the power of model systems, and that natural MICROCOSMS (see Glossary) are worth considering as such models (Box 1).

Model systems have three useful features: tractability, generality and realism [1], which enable future experiments to build on previous results. Ecologists have

adopted many systems that meet some but not all of these requirements. For example, laboratory-assembled communities of protozoa enable quick, precise and highly replicated experiments (i.e. have high tractability) [2,3], but have been criticized for their artificiality (i.e. have potentially low generality) [4]. Whole-ecosystem experiments represent the opposite extreme: entire natural communities (i.e. are highly realistic) whose large size usually necessitates poorly replicated, long duration and mechanistically simple studies (i.e. have potentially low tractability). There has been heated debate about the apparent merits of 'replication versus realism' [5] in ecology. Natural microcosms potentially offer a way to circumvent this tradeoff between artificiality and tractability.

Natural microcosms are small contained habitats that are naturally populated by minute organisms (Figure 1). Examples include the protozoan and metazoan communities of aquatic PHYTOTELMATA (pitcher plants, bromeliads, treeholes, etc.), microarthropod communities of moss patches, micro-crustacean communities in rock pools,

## Glossary

**Bottom-up (effect):** the effect on a focal species, community or trophic level originating from changes at a lower trophic level.

**Mesocosm:** a contained subset of a larger ecological system, such as an aquarium filled with pond biota. Aquatic mesocosms are generally between 1 and 100 L in volume.

**Metacommunity:** a set of local communities that are linked by dispersal of multiple interacting species.

**Metapopulation:** a set of local populations of a single species that are linked by dispersal.

**Microcosm:** a small, contained ecological system, such as *Daphnia* in a rockpool. Aquatic microcosms are generally <1 L in volume.

**Phytotelmata:** a contained aquatic habitat formed naturally by a plant and populated by aquatic organisms. Examples include pitcher plants, *Heliconia* floral bracts, tree holes and bromeliads.

**Top-down (effect):** The effect on a focal species, community or trophic level originating from changes at a higher trophic level.

### Box 1. What type of model system?

Biological model systems involve the use of one biological system to represent another. Classic examples include the bacteria *Escherichia coli* for molecular biology, the pipid frog *Xenopus* for developmental biology, the house mouse *Mus musculus* for immunology and the fruit fly *Drosophila melanogaster* for genetics. Such models have proven to be powerful research tools.

Biological model systems correspond incompletely to the systems that they represent, but are similar enough in the salient features to be useful. For example, the nematode *Caenorhabditis elegans* is clearly different from humans in many respects, but both have a eukaryotic genome; thus, the small nematode genome is a useful model for understanding how the larger human genome might function. Such model systems fulfill a variety of functions. In some cases, the model system is viewed as a direct analog of another (target) system, because the latter cannot be ethically or practically examined (e.g. neuroscience experiments with mice to understand human cognition, and ecotoxicology studies in MESOCOSMS [35] to predict impacts of pollutants). In other cases, experiments with model systems screen hypotheses for subsequent testing with the target system (e.g. drug testing on animals is a prelude to, not a replacement of, drug testing on humans). Finally, some model systems are used for theory testing and development, with the proviso that the theory might need to be parameterized for other systems (e.g. evolution theory developed with *Drosophila* requires adjustments for selection coefficients and modes of inheritance before being applied to other organisms).

It is an open question as to whether natural microcosms serve as direct analogs of other ecological systems, but they can serve as scaled analogs [39,42]. This approach, in which rates are scaled to system size, offers considerable promise. For example, marine ecologists have derived empirical relationships that relate productivity to mesocosm size, which, when extrapolated to the scale of coastal systems, still provide remarkably good predictions [39]. Natural microcosms show additional, but untapped, promise for screening potential hypotheses before researchers commit resources to experiments in larger, slower systems (such as forests or lakes). For screening, there needs to only be rough concordance between the model and target systems such that effects seen in the model system (e.g. rock pools) are likely to be worth investigating in the target system (e.g. lakes). Finally, natural microcosms have been used extensively as systems for testing and developing theory, the focus of this paper.

invertebrate communities on mollusk shells, and beetles in fungal sporocarps. The research conducted in such habitats was recently the focus of a symposium at the Ecological Society of America Annual Meeting (August 2003, Savannah, GA, USA).

### The case for natural microcosms

Ecologists are often first drawn to natural microcosms for entirely practical reasons. These advantages can be summarized as small size, restricted movement and fast temporal dynamics.

Natural microcosms are all, by definition, small habitats. The small habitat size enables high replication in experiments, and thus sufficient power in observational studies to remove covariate effects statistically. Natural microcosms also tend to be contained habitats, that is, they have a clearly delineated arena for species interactions. Describing such local (or localized) communities is relatively simple. By contrast, food webs and communities in more continuous habitats tend to have 'fuzzy' boundaries, creating one of the oldest problems in ecology: the precise delineation of communities. Finally, experimental

manipulations of animal communities in continuous habitat are often complicated either by the unwanted movement of individuals into and out of the study arena, or by fence effects when movement is artificially constrained [6]. By contrast, the physical boundaries of natural microcosms (typically air–water, but also interfaces such as soil–rock) represent a natural constraint for biota, which facilitates the addition or removal of species [7–9] or even the reassembly of an entire community from scratch [10–12]. These manipulations in natural microcosms are usually maintained long enough for the purposes of many experiments. However, natural microcosms are not closed systems. Eventually, all manipulations will be altered by processes such as the emergence of adult insects, oviposition of eggs and colonization by microorganisms. Such dispersal processes among microcosms have their own value for answering questions about METACOMMUNITY dynamics.

The organisms in natural microcosms also tend to be small, typically including: insects and smaller arthropods (amphipods, mites, collembola, etc.), annelids, microcrustaceans (e.g. ostracods and *Daphnia*), metazoa and protozoa (e.g. rotifers, ciliates and flagellates) and bacteria. In the case of most microscopic organisms (<1 mm), the fast generation time enables experiments to run for many generations, allowing ecologists to test theory about both short- and long-term effects of manipulations with experiments that last only several weeks or months [11,13]. Experiments with larger organisms, by contrast, are sometimes criticized for only capturing short, transient dynamics, even when these experiments are conducted over several years [14].

### Questions best suited to natural microcosms

The usefulness of natural microcosms will depend not only on their properties, but also on the theoretical questions being addressed. All theory makes assumptions about the scale and importance of ecological processes. These assumptions might be met by only some natural microcosms, or by only some taxa in a natural microcosm, or not at all. For example, both rotifers and mosquitoes are found in pitcher plants (Box 2). However, rotifers complete their lifespan within an individual pitcher, whereas only the larval stages of mosquitoes occur in pitchers (the adults emerge and utilize the entire bog within which the pitcher is located). The drying of a pitcher can thus be used to study the effects of disturbance on METAPOPOPULATION dynamics for rotifers, but only local variation in survivorship for mosquitoes.

Recently, natural microcosms have proved to be ideally suited, in terms of scale and process, to testing two new and very active areas of ecological theory: the effect of declining diversity on ecosystem function, and the effects of neighbouring communities (the 'metacommunity') on species richness.

### Natural microcosms show promise for biodiversity–ecosystem function research

Community ecologists have recently focused on understanding the effect of species loss on the rates and stability of ecosystem functions. To date, most experiments have



**Figure 1.** Examples of natural microcosms. (a) aquatic insects in bromeliads (b) marine invertebrates colonizing pen shells (c) micro-arthropods in moss patches (d) beetles in fungal sporocarps (e) aquatic food webs in pitcher plants and (f) invertebrates and micro-crustaceans in rockpools. Reproduced with permission from D.S. Srivastava (a), P. Munguia (b), A. Gonzalez (c), S. Bondrup-Nielsen (d), T.E. Miller (e) and J. Kolasa (f).

involved assembling random subsets of monotrophic communities, such as grassland plants in 1-m<sup>2</sup> plots. Such manipulations of synthetic communities have been useful for the development of theory, but the current challenge is to extend these results to multitrophic food webs of coevolved species experiencing real patterns of species loss [15,16]. Natural microcosms have the potential to play a particularly important role at this stage of the diversity–function research program, because real local extinctions can be easily (and ethically) induced by changes in the habitat, and because responses can be tracked over multiple generations and through multiple trophic levels.

Local extinction has been experimentally induced by means of fragmenting moss patches, and the effects tracked in terms of microarthropod biomass [17]. Declines in community biomass were temporally decoupled from species extinctions because of two patterns: (i) rare microarthropod species were lost first with minimal impact on community biomass; and (ii) biomass was most affected by the declines in abundance of common species that foreshadowed their eventual extinction. This demonstrates that real patterns in extinctions might have a lag in affecting ecosystem function, causing a ‘functioning debt’ [17]. Adding corridors between the habitat fragments reduces both extinctions and the loss of function [17,18]

A second example is offered by diversity–stability studies in rock pools. Recent debate has focused on whether increased diversity can reduce variability in ecosystems, whether this reduction in variability is expected at population or community levels and under which conditions such an effect can occur [19]. By using natural variation between rock pools in faunal diversity, positive diversity–stability relationships have now been shown at both population and community levels, but only when the confounding effects of environmental variation [20] or habitat specialization [21] are removed.

In all of the above examples, natural microcosms have provided important ‘real world’ tests of diversity–function theory developed from synthetic communities, and suggest how theory can be modified to incorporate real patterns in extinctions or community assembly.

#### Natural microcosms enable tests of metacommunity theory

Natural microcosms are often embedded in a hierarchical spatial structure (Box 2), which is ideally suited to test metacommunity theory. The crucial insight of metacommunity theory is that a single (‘local’) community can be significantly affected by dispersal and extinction events in the surrounding region. Metacommunities are often, but not necessarily, modeled as arrays of patches, with one community per patch. Such models are well approximated

### Box 2. Pitcher plant communities and hierarchical spatial structure

Each pitcher, or water-filled leaf, of a pitcher plant contains a discrete food web consisting of aquatic insects and microscopic organisms (a food web from Eastern Canada [43] is shown in Figure 1). The basal energy for this food web is provided by the carcasses of drowned terrestrial insects. The pitcher plant illustrated, *Sarracenia purpurea*, contains ca. 3–12 such pitchers per plant. *Sarracenia* pitcher plants occur near other pitcher plants within the same bog, and bogs often occur near other bogs in the landscape. Thus, the processes that affect a pitcher plant food web occur in a hierarchical order of spatial scale, from pitchers to plants to bogs to region [43–45].

At the local (pitcher) scale, species diversity of many microscopic organisms (bacteria, rotifers and protozoa) is strongly affected by both TOP-DOWN (mosquito occurrence) and BOTTOM-UP (carcass provisioning) processes [7,9,13,22,46]. Mosquito occurrence at the pitcher scale is affected by bottom-up effects, such as carcass provisioning [43], carcass processing by midges [47] and pitcher size [43,48]. Importantly, these local effects on mosquito occurrence are modified by landscape-scale features, such as pitcher density and location [43,48,49], probably because of the behaviour of adults during oviposition [43,49]. Going one scale larger, differences between bogs in pitcher plant arthropods are related to features such as bog size, isolation and exposure [48,49], and reflect processes of colonization and population extinction. Finally, at the continental (North America) scale, highest protozoan and bacterial richness occur at the highest latitudes [44]. This unusual pattern is linked to climatic limits to the northern range of the mosquito [44] and, thus, ultimately to the same top-down processes seen at the local level.

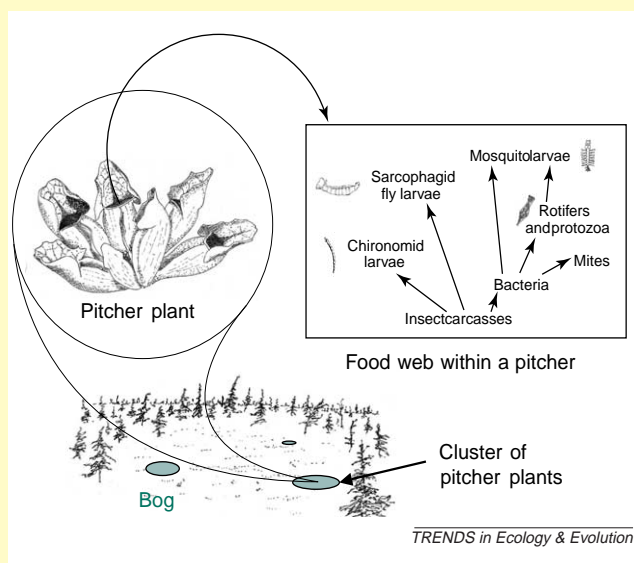


Figure 1.

in nature by clusters of natural microcosms. It is also relatively easy to manipulate crucial parameters in natural microcosms, such as species richness per patch, dispersal rate and spatial structure. For example, dispersal between natural microcosms has been modified by adding corridors (e.g. between patches of moss [17,18]) or by experimental additions (e.g. rotifers and protozoa pipetted between pitcher plants [22] or seeds added to riverine tussocks [12]). Researchers have laid out groups of marine pen shells [23,24] and fungal-sporocarps [25,26] in different patterns to examine the effects of spatial structure (e.g. number of patches, distance between patches) on the invertebrates inhabiting these natural

microcosms. To date, some of the best experimental tests of metacommunity theory have come from natural microcosms, as illustrated by these next three examples.

Several metacommunity models assume that the extinction rate in a patch increases with patch species richness (e.g. [27]). This was first demonstrated experimentally using *Daphnia* communities of coastal rock pools [11]. Metacommunity models also often assume that colonization rate increases with the number of neighbouring patches; there is also evidence from coastal rockpools for this effect [27]. Interestingly, in desert rockpools [28], local richness can be adequately modeled without requiring competition to cause extinctions; rather, local richness is a dynamic equilibrium between colonization from the surrounding region and extinction resulting from desiccation.

In a second metacommunity model [29], local diversity is predicted to be maximized at intermediate levels of dispersal. At low dispersal rates, dominant competitors exclude other species, whereas, at high dispersal rates, the species with low dispersal abilities are unable to persist regionally, reducing local richness. The first test of this model was carried out in pitcher plants, and involved manipulating the dispersal rate of microorganisms by pipetting specific water volumes between pitchers [22]. Local diversity was highest at intermediate dispersal rates, as predicted by the model, but this pattern disappeared in the presence of predators [22]. A related model [23] predicts that the strongest correlation between local and regional richness will occur at intermediate assembly times. Recent work [24] with marine organisms assembling on pen shells supports this prediction, but only for the motile organisms, suggesting that dispersal mode must be considered.

A third group of models [30,31] have shown that species co-existence at the metacommunity level can be facilitated not only by local effects, such as resource heterogeneity, but also by larger scale effects, such as patterns of spatial aggregation. As aggregation of the superior competitor increases, it occupies fewer patches, creating a probabilistic refuge for inferior competitors. Some of the best evidence for the aggregation hypothesis has come recently from natural microcosms, specifically insect larvae in fungal sporocarps [32,33], carrion [31] and fallen fruit [30,34].

### Microcosms: why go natural?

Many of the practical advantages that we have described for natural microcosms apply just as well to artificial microcosms (e.g. beaker and bottle experiments) [2]. Indeed, it could be argued that artificial microcosms have further advantages [3,35], as the even greater control of habitat enables very subtle effects to be detected with reasonable power. However, the main criticism of beaker experiments has never been tractability, but rather the general applicability of the results. Naeem [36] describes artificial microcosms as having high 'internal validity' (defined as transparency of mechanisms, and similarity to theoretical constructs) but low applicability to natural ecosystems, or 'external validity'. For example, artificially assembled communities do not represent

coevolved or co-occurring taxa with natural abundance distributions. Thus, artificial and natural microcosms ask complementary questions: artificial microcosms tell us if hypothesized effects can occur, whereas natural microcosms tell us if such effects do occur and are important.

### But can we generalize from natural microcosms?

One could argue that the very features that make natural microcosms unusually tractable, such as small size and discrete boundaries, also make them ecological oddballs. This could limit our ability to generalize to other systems, particularly the larger systems upon which human societies are disproportionately focused. For example, it could be argued that the small size of natural microcosms could make them particularly prone or sensitive to disturbance. Freezing, drought and treefall can have catastrophic effects on the fauna of individual treeholes [37] but minor effects on the larger forest ecosystem. In a rock pool, diurnal variation in temperature exceeds that in a large body of water [38]. Organisms often cannot flee these disturbances because of the discrete boundaries; larval aquatic insects, for example, are trapped in a drying treehole [37]. One could argue, therefore, that the ecology of natural microcosms will be dominated by non-equilibrium dynamics, in which dispersal, local extinction and spatial structure play key roles. There are two counter-arguments to this proposition. First, such processes are probably important in all communities, just more evident in a contained and rapidly changing system. Second, most taxa in natural microcosms have short generation times. Once dispersal and disturbances are scaled by generation times, there might be little difference in their frequency or intensity between natural microcosms and any other system, including larger systems [39]. Spatial effects could be similarly scaled by body size of the organisms involved. Unfortunately, this type of biological scaling has rarely been investigated by ecologists, but is a fertile area for future research (Box 3). Such information would determine to what degree results from natural microcosms could be compared to those from larger areas, such as human-dominated landscapes.

These effects of system size are a double-edged sword, not only limiting the scaling-up of results from small systems to large systems, but also the applicability of large system studies to smaller systems. The onus is not only on ecologists who work with small systems to prove the relevance of their results to larger systems, but also the reverse. If a general ecological theory does not apply to natural microcosms, or to lakes, or to any common type of ecosystem, then it is, by definition, not general. The challenge is to develop theory applicable to a range of ecosystem sizes.

### Conclusions: are natural microcosms potential model systems?

Recent research with natural microcosms has had a particularly large impact. However, to be embraced as model systems, natural microcosms must demonstrate advantages over other ecological systems. Huston [40] suggests that some ecological systems are more suitable

### Box 3. Questions for future research with natural microcosms

#### How do ecological processes change with system size?

This question is crucial to resolving exactly how knowledge gleaned from natural microcosms can be extrapolated to other systems. For example, if respiration, food-web structure, dispersal rates or environmental variability shift consistently from rock pools one liter in size to small ponds of 100 l, we could directly compare results from any of these systems after a volume correction. The answer to these questions might be most useful when expressed in biologically relevant time units (e.g. generation lengths) rather than in absolute time units (days).

#### Do species characteristics and interactions drive patterns at all spatial scales?

Neutral models of diversity suggest that, at all scales, regional processes of dispersal and speciation are much more important than are species characteristics and interactions in creating species abundance patterns. Species saturation theory posits that species interactions are more important than such regional processes in limiting local diversity. Natural microcosms might be particularly useful in testing these ideas, because regional processes and macroecological patterns can be examined at practical spatial scales (e.g. dispersal beyond a few meters might be rare for taxa in rockpools [27]).

#### What processes are most crucial for species conservation?

Conservation theory is often difficult to test experimentally without endangering the taxa that we wish to conserve. Natural microcosms can serve as model systems for testing conservation theory, because there is little consequence of local extinction for their generally widespread taxa. For example, natural microcosms are well suited to experiments examining the effects of exotic species, because the trophic level, order and immigration rate of the introduced species can be tightly controlled, with numerous replicates.

#### How does evolution influence community dynamics?

Several studies in artificial microcosms have demonstrated that evolution can affect community dynamics by operating on a similar timescale to ecological processes [3]. Natural microcosms present an opportunity to test the importance of evolutionary processes on community dynamics in a naturally assembled system.

for quick tests of conceptual models, and others for model verification (i.e. comparing conceptual theory with natural reality). Artificial microcosms are well suited to theory testing [3,35], and entire-ecosystem experiments are well suited to verifying the applicability of models to complex natural systems. Natural microcosms, however, fill both roles in ecology by providing rapid and realistic field tests of key ecological theories and, as such, should be primarily viewed as interesting ecosystems in their own right. Specifically, natural microcosms share common features with other real ecosystems (e.g. complex interactions between co-evolved members), but also with theoretical models (a few species with known growth and dispersal parameters). Thus, they can act as 'halfway houses' [41] between theory and the vast array of real ecosystems. This potential will only be realized when we optimize the types of question that we address with natural microcosms (Box 3). Natural microcosms will be particularly effective in testing the most general facets of ecological theory whenever they require a degree of complexity (e.g. indirect interactions, number of species, habitat unpredictability) that is unknown and thus difficult to reproduce via

mathematical models or in artificial systems. Although this certainly does not mean that ecologists should cease to study either large-sized ecosystems or artificial assemblages, it does suggest that we should be making much more use of the opportunities offered by natural microcosms.

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### References

- Levins, R. (1984) The strategy of model building in population biology. In *Conceptual Issues in Evolutionary Biology* (Sober, E., ed.), pp. 18–27, Cambridge University Press
- Lawler, S.P. (1998) Ecology in a bottle: using microcosms to test theory. In *Experimental Ecology: Issues and Perspectives* (Reserits, W.J. Jr and Bernardo, J., eds), pp. 236–253, Oxford University Press
- Jessup, C.M. *et al.* (2004) Big questions, small worlds: microbial model systems in ecology. *Trends Ecol. Evol.* 19, 189–197
- Carpenter, S.R. (1996) Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* 77, 677–680
- Schindler, D.W. (1998) Replication versus realism: the need for ecosystem-scale experiments. *Ecosystems* 1, 323–334
- Krebs, C.J. (1996) Population cycles revisited. *J. Mammal.* 77, 8–24
- Kneitel, J.M. and Miller, T.E. (2002) Resource and top-predator regulation in the pitcher plant (*Sarracenia purpurea*) inquiline community. *Ecology* 83, 680–688
- Fincke, O.M. *et al.* (1997) Predation by odonates depresses mosquito abundance in water-filled tree holes in Panama. *Oecologia* 112, 244–253
- Miller, T.E. *et al.* (2002) Effect of community structure on invasion success and rate. *Ecology* 83, 898–905
- Srivastava, D.S. and Lawton, J.H. (1998) Why more productive sites have more species: an experimental test of theory using tree-hole communities. *Am. Nat.* 152, 510–529
- Bengtsson, J. (1989) Interspecific competition increases local extinction rate in a metapopulation system. *Nature* 340, 713–715
- Levine, J.M. (2001) Local interactions, dispersal, and native and exotic plant diversity along a California stream. *Oikos* 95, 397–408
- Miller, T.E. *et al.* (2002) Trophic interactions in the phytotelmata communities of the pitcher plant, *Sarracenia purpurea*. *Commun. Ecol.* 3, 109–116
- Tilman, D. (1989) Ecological experimentation: strengths and conceptual problems. In *Long-Term Studies in Ecology* (Likens, G.E., ed.), pp. 136–157, Springer-Verlag
- Duffy, J.E. (2003) Biodiversity loss, trophic skew and ecosystem functioning. *Ecol. Lett.* 6, 680–687
- Srivastava, D.S. (2002) The role of conservation in expanding biodiversity research. *Oikos* 98, 351–360
- Gonzalez, A. and Chaneton, E.J. (2002) Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. *J. Anim. Ecol.* 71, 594–602
- Gonzalez, A. *et al.* (1998) Metapopulations dynamics, abundance, and distribution in a microecosystem. *Science* 281, 2045–2047
- McCann, K.S. (2000) The diversity–stability debate. *Nature* 405, 228–233
- Romanuk, T.N. and Kolasa, J. (2002) Environmental variability alters the relationship between richness and variability of community abundances in aquatic rock pool microcosms. *Ecoscience* 9, 55–62
- Kolasa, J. and Li, B.-L. (2003) Removing the confounding effect of habitat specialization reveals the stabilizing contribution of diversity to species variability. *Proc. R. Soc. Lond. Ser. B* 270 (Suppl.), S198–S201
- Kneitel, J.M. and Miller, T.E. (2003) Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. *Am. Nat.* 162, 165–171
- Mouquet, N. *et al.* (2003) Community assembly time and the relationship between local and regional richness. *Oikos* 103, 618–626
- Munguia, P. (2004) Successional patterns on pen shell communities at local and regional scales. *J. Anim. Ecol.* 73, 64–74
- Starzomski, B.M. and Bondrup-Nielsen, S. (2002) Analysis of movement and the consequence for metapopulation structure of the forked fungus beetle, *Bolitotherus cornutus* Panzer (Tenebrionidae). *Ecoscience* 9, 20–27
- Heard, S.B. (1998) Resource patch density and larval aggregation in mushroom-breeding sites. *Oikos* 81, 187–195
- Hanski, I. and Ranta, E. (1983) Coexistence in a patchy environment: three species of *Daphnia* in rock pools. *J. Anim. Ecol.* 52, 263–279
- Kiflawi, M. *et al.* (2003) The relative impact of local and regional processes on macro-invertebrate species richness in temporary pools. *J. Anim. Ecol.* 72, 447–452
- Mouquet, N. and Loreau, M. (2002) Coexistence in metacommunities: the regional similarity hypothesis. *Am. Nat.* 159, 420–426
- Inouye, B.D. (1999) Integrating nested spatial scales: implications for the coexistence of competitors on a patchy resource. *J. Anim. Ecol.* 68, 150–162
- Ives, A.R. (1991) Aggregation and coexistence in a carrion fly community. *Ecol. Monogr.* 61, 75–94
- Wertheim, B. *et al.* (2000) Species diversity in a mycophagous insect community: the case of spatial aggregation vs. resource partitioning. *J. Anim. Ecol.* 69, 335–351
- Toda, M.J. *et al.* (1999) Coexistence mechanisms of mycophagous drosophilids on multispecies fungal hosts: aggregation and resource partitioning. *J. Anim. Ecol.* 68, 794–803
- Krijger, C.L. and Sevenster, J.G. (2001) Higher species diversity explained by stronger spatial aggregation across six neotropical *Drosophila* communities. *Ecol. Lett.* 4, 106–115
- Taub, F.B. (1997) Unique information contributed by multispecies systems: examples from the standardized aquatic microcosm. *Ecol. Appl.* 7, 1103–1110
- Naeem, S. (2001) Experimental validity and ecological scale as criteria for evaluating research programs. In *Scaling Relations In Experimental Ecology* (Gardner, R.H. *et al.*, eds), pp. 223–250, Columbia University Press
- Sota, T. *et al.* (1994) Habitat stability and the larval mosquito community in treeholes and other containers on a temperate island. *Res. Popul. Ecol.* 36, 93–104
- Therriault, T.W. and Kolasa, J. (1999) Physical determinants of richness, diversity, evenness and abundance in natural aquatic microcosms. *Hydrobiologia* 412, 123–130
- Petersen, J.E. *et al.* (2003) Multiscale experiments in coastal ecology: improving realism and advancing theory. *Bioscience* 53, 1181–1197
- Huston, M.A. (1999) Microcosm experiments have limited relevance for community and ecosystem ecology: synthesis of comments. *Ecology* 80, 1088–1089
- Lawton, J.H. (1995) Ecological experiments with model systems. *Science* 269, 328–331
- Schneider, D.C. (2001) Spatial allometry: theory and application to experimental and natural aquatic ecosystems. In *Scaling Relations In Experimental Ecology* (Gardner, R.H. *et al.*, eds), pp. 113–153, Columbia University Press
- Trzcinski, M.K. *et al.* (2003) Colonisation of pitcher plant leaves at several spatial scales. *Ecol. Entomol.* 28, 482–489
- Buckley, H.L. *et al.* (2003) Reverse latitudinal trends in species richness of pitcher-plant food webs. *Ecol. Lett.* 6, 825–829
- Harvey, E. and Miller, T.E. (1996) Variance in composition of inquiline communities in leaves of *Sarracenia purpurea* L on multiple spatial scales. *Oecologia* 108, 562–566
- Cochran-Stafira, D.L. and Ende, C.N.V. (1998) Integrating bacteria into food webs: studies with *Sarracenia purpurea* inquilines. *Ecology* 79, 880–898
- Heard, S.B. (1994) Pitcher-plant midges and mosquitoes: a processing chain commensalism. *Ecology* 75, 1647–1660
- Miner, J.A. and Taylor, P.D. (2002) Effects of peatland size and exposure on two species of Diptera inhabiting the pitcher plant *Sarracenia purpurea* L. *Ecoscience* 9, 347–354
- Krawchuk, M.A. and Taylor, P.D. (2003) Changing importance of habitat structure across multiple spatial scales for three species of insects. *Oikos* 103, 153–161