

# Understanding Ecological Concepts: The Role of Laboratory Systems

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## I. INTRODUCTION

Ecology is a disparate discipline with studies ranging from the highly abstract to the highly applied. Understanding ecological concepts often involves the use of theoretical models, laboratory studies, and/or field studies, all of which exist on a continuum, with laboratory experiments often considered to be somewhere between abstract theoretical models and the field studies of the natural world. Laboratory systems have many appealing features such as ease of culturing, manipulation, minimal sampling difficulties, repeatability, and quantifiable resource supply, but there are more fundamental reasons for using laboratory microcosms.

Long-term population (time series) studies are the cornerstone for testing hypotheses about the processes and mechanisms of population regulation, limitation, and persistence. However, field studies of population ecology suffer from a double jeopardy. While ecological time series are at the heart of population ecological research, they are often of insufficient length and are unreplicated which makes statistical inferences often weak or even impossible. Laboratory experiments provide one solution to this jeopardy by allowing well-replicated, long-term experiments to be done under controlled environmental conditions. The use of laboratory or model systems in ecology has been widely advocated as a plausible and realistic approach to understanding the processes and mechanisms underpinning ecological systems (Kareiva, 1989; Lawton, 1995).

In this review, we discuss the use of laboratory microcosms in understanding ecological concepts focusing particularly on the ideas central to population ecology. However, our rationale and approach is equally applicable to evolutionary and genetic experiments, and can be more widely applied in the design and implementation of field-based ecological experiments. We begin by outlining the philosophy and rationale for laboratory microcosm experiments. We emphasize the role of appropriate model selection and choice as the underlying approach for integrating ecological theory and experiments. Following this, we review the historical contributions that laboratory experiments have made to our understanding of a number of core ecological concepts. In the final section, we conclude by examining the prospects for the use of laboratory systems in ecological research.

## II. RATIONALE

There are some pertinent philosophical prerequisites placed on the rationale for the use of laboratory microcosm experiments. For inference and belief in an ecological phenomenon or particular result, it is essential from the outset that a distinction is made between proof and evidence. Proof shows that if  $x$  is so, then  $y$  is also so, while evidence shows that given  $x$ ,  $y$  is probably so. The difference between proof and evidence rests in the accumulation of scientific beliefs which has important implications in ecological research. However, both proof and evidence require an  $x$  to start, and knowledge ultimately relies on some scientific truths that are known without proof or evidence.

One philosophical view is that we should derive ecological axioms from empiricism (the collation of ecological knowledge). Such empiricism is based on experience; by pooling evidence found through experience, patterns can be described and predicted. Under empiricism, scientific methods and rules are used to identify genuine from spurious patterns. Although the methods may be complex (e.g., analytical models, statistics), the rules are relatively

straightforward. Hypotheses are formulated, data are collected and predictions are made. Acceptance is the verdict of further experiences that is eventually generalized to scientific theorems or the derivation of axioms. However, this approach may be too simplistic (even with the concepts of modern mathematics and statistics) as it is more geared towards predictive success than telling the genuine ecological patterns from spurious ones. A second view is that of rationalism, which involves explaining the ecological pattern and finding the mechanistic cause. Such an approach to ecological research often focuses on pragmatic reasons for asking a particular question.

However, it may be preferable to take a different approach with ecological studies and reject the assumptions of both rationalism and empiricism. Rather than passively recording ecological patterns, an active judgment is required to reject or amend a hypothesis. The ideal then becomes one of model evaluation using data and assessing how much a model is 'worth'. For example, how relevant is the model at explaining the ecological phenomenon under scrutiny? Is it simple enough? Is it realistic? By taking this approach of model selection and choice, any discoveries made are only those which reason (defined in terms of statistical power or inference) will finally certify. If laboratory experiments are to contribute to the falsification of hypotheses in strict Popperian fashion, then it is of paramount importance in ecological research that the 'worth of the model' is clearly known. While it is obvious that these philosophical approaches (rationalism, empiricism, Popperian) are not mutually exclusive, it is clear that the use of laboratory microcosms systems or organisms requires a sensible frame of reference against which to base a scientific rationale.

## **A. Model Choice**

One frame of reference is through the use and selection of the most appropriate model for data. This is the model that best approximates the data and allows inference on the most likely ecological effects (model parameters) supported by the data. Models are an approximation, and understanding the methods of model choice and selection are of overriding importance. While advocated as a robust alternative to standard Popperian hypothesis testing (Burnham and Anderson, 2002), the application of model selection approaches (e.g., through the use of information-theoretic criteria) remains relatively under-utilized in ecology. In this chapter, we advocate fitting different explanatory models under the principles of parsimony (that is, the model should be as simple as possible) and place less emphasis on merely testing null hypotheses. Given the advancement in ecological theory (May, 1981; Gurney and Nisbet, 1998; McGlade, 1999; Murdoch *et al.*, 2003a), mathematical models abound in ecology and, in particular, in population

**Table 1** Candidate models used to describe density-dependent processes in single-species populations (May and Oster, 1976, Bellows, 1981). Models are fitted using a Gaussian likelihood (equation 5) to time-series data. The most parsimonious description of the dynamics is based on the log-likelihood values by evaluating AIC (equation 1). Model comparison is made by computing the difference between the most parsimonious model (model 2) and the  $i^{\text{th}}$  model

	Model	AIC	$\Delta_i (AIC_i - AIC_{\min})$
1	$dN/dt = r \cdot N_t - b \cdot \log(N_t) \cdot N_t$	2566.438	5.516
2	$dN/dt = r \cdot N_t - \log(1 + a \cdot N_t) \cdot N_t$	2560.922	-
3	$dN/dt = r \cdot N_t - a \cdot N_t \cdot N_t$	2611.352	50.43
4	$dN/dt = r \cdot N_t - (a \cdot N_t^b) \cdot N_t$	2566.952	6.03
5	$dN/dt = r \cdot N_t - b \cdot \log(1 + a \cdot N_t) \cdot N_t$	2582.214	21.292
6	$dN/dt = r \cdot N_t - \log(1 + (a \cdot N_t)^b) \cdot N_t$	2570.676	9.754

ecology. As an illustration of this, a range of continuous-time models for density dependence are listed in Table 1. These represent a variety of ecological processes and mechanisms that may underpin the dynamics of a single-species population. However, the link between these candidate models and empirical data remains relatively weak. Although much is known about these models and laboratory experiments on density dependence (see section titled Density Dependence), there has been little development in assessing which model (density-dependent process) may best describe an ecological system.

In attempting to find the model that best describes or approximates an ecological problem (data), then in some sense it is most appropriate to consider the model that minimizes information loss (Burnham and Anderson, 2002). This is most straightforwardly achieved through the use of information-theoretic criteria, such as the Akaike Information Criterion (AIC) (Akaike, 1973, 1974). This criterion is based on the likelihood of each model given the data ( $L(\text{model}|\text{data})$ ) and is a bias-corrected (in terms of the number of parameters estimated from the data) maximum log-likelihood value:

$$AIC = -2 \cdot \log(L(\text{model}|\text{data})) + 2 \cdot np, \quad (1)$$

where  $np$  is the number of parameters estimated in the model. Of critical importance in model choice is obtaining a small set of candidate models that capture the ecological problem at hand. Once an appropriate set of models have been chosen, competing models (hypotheses) can be ranked by determining relative AIC values (based on the difference to the minimum AIC value). These methods of model choice and selection using information-theoretic approaches are an extension of simple parameter estimation optimization problems (e.g., minimizing the log-likelihood) (Burnham and Anderson, 2002) and are amenable to development within the scope of ecological research problems. Within these schemes, methods now exist

that allow selection, uncertainty and inference from multiple models to be considered. It is often the case that more than one theoretical ecological model adequately explains a problem. Within the information-theoretic paradigm, approaches exist for examining multiple models and making formal inference from more than one process. Determining the weighted evidence of one model over another (similar to likelihood ratio tests) has been widely advocated as a robust, simple, and useful approach for providing information on contrasting (ecological) effects (Burnham and Anderson, 2002).

To illustrate the rationale of model selection as a plausible approach for inferring ecological processes and mechanisms, we consider the density-dependent models in Table 1 as the candidate models for the population dynamics of *Drosophila ananassae* illustrated in Fig. 1A. To explain the approach, we take a straightforward description of a density-dependent interaction:

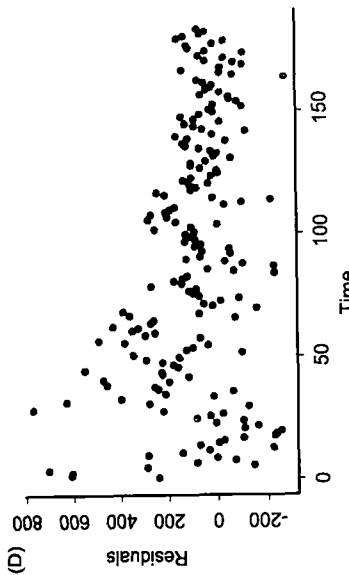
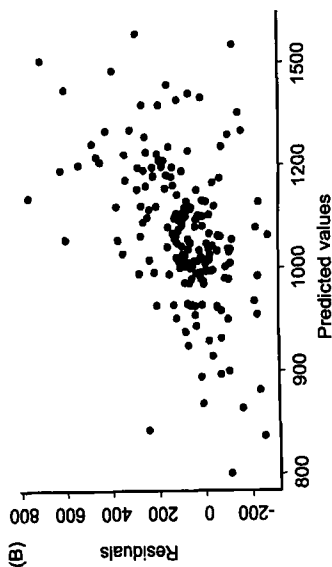
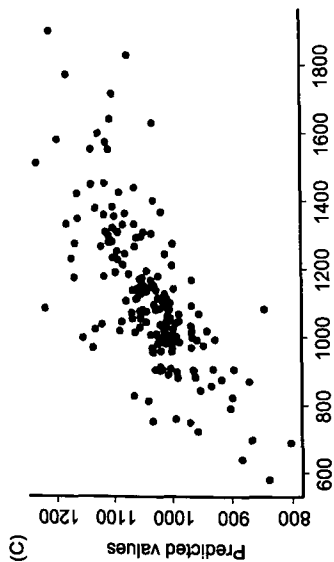
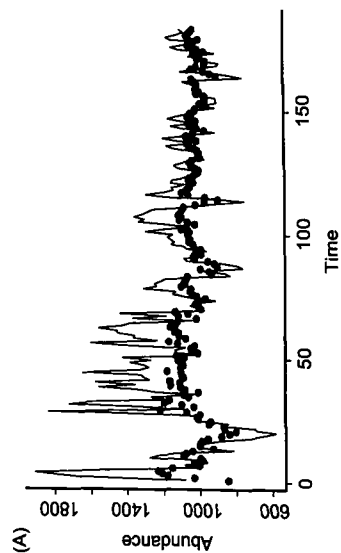
$$\frac{dN}{dt} = r \cdot N_t \cdot \left(1 - \frac{N_t}{K}\right) - d \cdot N_t, \quad (2)$$

where  $r$  is the population rate of increase,  $K$  is the population carrying capacity, and  $d$  is the natural mortality rate. To determine the expected number of individuals at the next census point ( $E_{n[i]}$ ) in the time series, this equation is solved over a fixed time period ( $t \rightarrow t + \tau$ ) corresponding to the census interval ( $\tau$ ):

$$E_{n[i]} = \int_t^{t+\tau} \left[ r \cdot N_t \cdot \left(1 - \frac{N_t}{K}\right) - d \cdot N_t \right] \cdot dx. \quad (3)$$

In order to contrast different density-dependent mechanisms, we use a maximum likelihood-based approach. In order to implement this, we need to give explicit consideration to the role of stochasticity on the dynamics. Given that the abundances of *D. ananassae* are estimates of adult flies alive at each census point, we assume that the variability in population size is due to a general environmental component of noise (rather than any particular demographic process). This is a straightforward way to capture a variety of noise processes and the different forms of stochasticity and their statistical implementation are outlined more fully elsewhere (Bonsall and Hastings, 2004). Under environmental noise, changes in population size between successive time intervals occur due to the deterministic processes of births and deaths, and the effects of random noise (acting additively on a log-scale) (Dennis *et al.*, 1995). The stochastic version of the logistic density-dependent model (equation 3) under environmental noise is:

$$E_{n[i]} = \exp(v) \cdot \int_t^{t+\tau} \left[ r \cdot N_t \cdot \left(1 - \frac{N_t}{K}\right) - d \cdot N_t \right] \cdot dx, \quad (4)$$



where  $v$  is an independent, identically distributed random variable with mean 0 and variance  $\sigma^2$ . It is assumed that the autocovariances between successive time points are small (autocorrelations are relatively weak) and as such are assumed to be uncorrelated. The appropriate likelihood is based on a univariate Gaussian probability distribution (Johnson *et al.*, 1994) and is of the form:

$$L(F) = \prod_{i=1}^z \frac{1}{\sqrt{2\pi}} \cdot \exp \left[ -\frac{1}{2} \left( \frac{N_{[i]} - E_{n[i]}}{\sigma} \right)^2 \right] \quad (5)$$

where  $N_{[i]}$  is the observed numbers of individuals at each census point  $i$  and  $E_{n[i]}$  is the expected number of individuals (determined from the integrated logistic model, equation 3) at each census point  $i$ . Given that the autocovariances are small, the overall likelihood is simply the product over all census points ( $z$ ). Maximum likelihood estimates of the parameter set ( $F$ ) are those that minimize the negative log-likelihood of equation 5. To compute this likelihood, an optimization method incorporating a numerical integration routine is implemented (Bonsall and Hastings, 2004).

As outlined in the previous text, models for the population dynamics can be contrasted and ranked by rescaling AIC values by simple differences (Burnham and Anderson, 2002). For this time series (Fig. 1A), Skellam's model (Skellam, 1951) has the most support for explaining the dynamics. Two models (Varley and Gradwell, 1960; Bellows, 1981) with intermediate AIC values ( $\Delta_i = 4 - 9$ ) have some support while three models (Ricker, 1954; Maynard-Smith and Slatkin, 1973; Hassell, 1975) have no support for explaining the population dynamics (with  $\Delta_i > 10$ ). Skellam's model is of the form:

$$\frac{dN}{dt} = r \cdot N_t - \log(1 + a \cdot N_t) \cdot N_t \quad (6)$$

where  $r$  is the population growth rate and  $1/a$  is a measure of the threshold above which competition for resources occurs. This form of intraspecific

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**Figure 1** Population dynamics of *Drosophila ananassae*. *D. ananassae* has a life-cycle of about 8 days, populations estimates were sampled every 3.5 days and, in chronological order, 4 resource patches (apple-based media) out of 20 were renewed every week. Model fitting and selection criteria reveal that the dynamics of *D. ananassae* are influenced by a density-dependent process and information-theoretic model selection criteria reveal that the functional form for the density dependence is  $\mu(N) = \log(1 + 0.001 \cdot N_t)$ . (A) Population dynamics (solid line) and one step-ahead predictions (solid circles) from the best-fitting model. (B to D) Post-model selection diagnostics show the (B) predicted values versus residuals, (C) correlation between observed and predicted abundances ( $\rho = 0.719$ ), and (D) residuals versus time. These diagnostics confirm that the assumptions about the error structures are appropriate.

competition suggests that the ecological mechanism underpinning the dynamics of *D. ananassae* is determined by a density-dependent process operating above a threshold density of about 1,000 flies. To ensure that the assumptions about the errors are appropriate, goodness of fit criteria (standardized residual plots, model one-step ahead prediction) are estimated for the likelihood function (equation 5). For the most parsimonious model of *D. ananassae* dynamics (equation 6), model selection diagnostics are illustrated in Fig. 1B to D.

Model choice (based on a maximum-likelihood approach, information-theoretic criteria, and post-selection diagnostics) motivates a departure from simple hypotheses testing for contrasting ecological effects. This holds the potential for exciting developments in population ecology through the combined, iterative approach of theoretical model predictions, manipulative and observational experiments, and robust statistical assessment and inference.

## B. Simplicity

Laboratory experiments and microcosms are often cited as simple analogs of nature where the ability to control environmental variables allows key theories to be tested. However, simplicity is too often equated with lack of relevance. Ecological laboratory systems have clear relevance and are not simply caricatures of nature. One way in which complexity can be incorporated into laboratory systems is by developing microcosms in which modules (small number of species interactions) can be assembled into larger groups of interacting species (Neill, 1975; Naeem *et al.*, 1994; Weatherby *et al.*, 1998). Such systems are not simple. Complicated environments, the availability of resource patches, and spatial heterogeneity all introduce levels of complexity into laboratory experiments (e.g., Huffaker *et al.*, 1963) that allow the ecological detail of nature to be approximated. Even one of the central practicalities, the control over environmental variables, can be manipulated in laboratory experiments to test the complex role of stochasticity and abiotic fluctuations on species interactions.

Laboratory experiments are not simple analogs of nature nor are they simple extensions of theoretical models. They provide a robust and rational approach for ecological research, provided it is accepted that they cannot be conducted on inappropriate scales of space or time, that one does infer from them experimental response of manipulating entire ecosystems (Carpenter *et al.*, 1995) and that they are not simply extrapolated to the field.

## C. Risk and Reward

Advancement in scientific understanding involves combining risk and reward. Risk can be defined as the likelihood that the objectives or aims of a



study will fall short of expectations. Such failure might arise because of the inappropriateness of the methods: poor selection of model, organisms, or question. Risk may also be expressed in terms of the (ecological) costs of the experiment. Such costs might arise through the manipulation of rare or endangered habitats. While the risks associated with ecological experiments are real, laboratory experiments allow risks to be minimized and reward maximized through the ability to manipulate, replicate, and infer on particular research questions.

For example, whole ecosystem experiments are often undertaken to assess a response rather than to falsify hypotheses. Such perturbations could be considered to have a high element of risk. The lack of replication limits the power that such experiments have in the comparison of models or competing hypotheses. Laboratory systems might circumvent some of these problems by allowing appropriate models and hypotheses to be tested and/or compared. However, even laboratory microcosms are not without risk. For example, laboratory-based systems are often used to explore the long-term dynamics of populations (e.g., Nicholson, 1954; Costantino *et al.*, 1995, 1997) and while the level of replication and manipulation extend the statistical power of such experiments, problems of methodology and inference still remain. For instance, statistical inference from population time series is often based on the measures of covariance such as autocorrelation and partial autocorrelation (e.g., Turchin, 1990). It is argued that patterns in these correlations are indicative of exogenous or endogenous dynamics and provide ideas about the period of oscillations (Nisbet and Gurney, 1982). However, poor experimental design (e.g., resource renewal regimes on a period equivalent to the generation time of the organisms) or weak statistical inferences can bias the interpretation of such data and introduces elements of risk into laboratory systems. Risk and failure through the poor selection of models, organisms, or questions have clear implications for how we approach ecological research questions with laboratory microcosms. In the next section, we review how a number of ecological concepts have been advanced by judicious choice and implementation of particular laboratory systems.

### III. CONCEPTS IN POPULATION ECOLOGY

Several concepts in population ecology have been shaped by the interplay between theoretical model development and experiments. In this section, we give an eclectic history of four broad ecological concepts (density dependence, competition, predation, and stability-complexity). For each concept, we introduce the core ecological theory and highlight how laboratory experiments and microcosms have been used to advance each area. In

general, we illustrate how laboratory microcosms have been used in testing hypotheses rather than comparing contrasting models. However, we use examples from a recent series of experiments to illustrate how these two approaches can be combined to provide a more rigorous understanding of a particular ecological problem and, more generally, demonstrate the rationale for laboratory experiments in ecological research.

### A. Density Dependence

Five broad concepts can be considered to be at the center of population ecology. These are: 1) population growth, 2) population equilibrium, 3) limitation, 4) regulation, and 5) persistence. Population growth is defined as the change in population size from one generation to the next. A population is at equilibrium if it does not change in size over time. Limitation is the process that sets the equilibrium, and regulation is the process by which a population returns to its equilibrium. Regulatory processes act in a density-dependent manner, and long-term population persistence requires that density-dependent processes operate. It is clearly evident that density-dependent processes can affect each of these concepts. Quite simply, density dependence is an increase in mortality or reduction in natality as population density increases.

### B. Nicholson's Concepts

Using studies from laboratory populations on *Drosophila* (Pearl, 1928) and *Tribolium* (Chapman, 1928; Holdaway, 1932), Nicholson (1933) conceptualized the idea of regulation through density-dependent processes. Particularly influential in Nicholson's ideas of regulation was the work on *Tribolium* by Holdaway (1932). Holdaway illustrated that *Tribolium* populations reached an equilibrium and persisted about this equilibrium. He argued that it was the interaction between the insects themselves that acted to maintain this persisting population, while the combination of physical environmental factors limited the population. Developing this theme, Nicholson lucidly argued that density dependence must be manifest through the effects of intraspecific competition since 'if the severity of its [competition] action against an average individual increases as the density of animals increases, the decreased chance of survival, or of producing offspring, is clearly brought about by the presence of more individuals of the same species in the vicinity' (Nicholson, 1933). This theme has been the focus of a wide range of laboratory population-dynamic experiments to explore the ideas of density dependence and population regulation.

To corroborate the conceptual ideas of density dependence, Nicholson conducted a series of laboratory experiments using *Lucilia cuprina*

(Nicholson, 1954, 1957). By defining concepts such as 'scramble' and 'contest' as various forms of intraspecific competition, Nicholson highlighted that these two mechanisms might have different consequences for the dynamics of a population. *Lucilia cuprina* was shown in a separate experiment to experience scramble competition such that some, and at times all, of the resources were insufficient to support the individuals in the population. Nicholson's population dynamic experiments (under different feeding regimes) showed that large amplitude cycles occurred rather than regulation to an equilibrium through density-dependent processes. In contrast to a recent criticism of this interpretation (Mueller and Joshi, 2000), these findings are quite succinctly defined in terms of Nicholson's mechanisms of intraspecific competition. Observations on the relatively high fecundity of *L. cuprina*, the time-delay in the effects of adult recruitment, and the fact that adult recruitment was highly non-linear, may actually be more precursory to developments in non-linear population dynamics rather than clarifying the theory associated with regulation and density dependence. Advances in non-linear population dynamics have been motivated by detailed analysis of laboratory microcosm systems. For example, in an investigation of non-linear population dynamics, Hassell *et al.* (1976a) examined the role of density dependence in the regulation of 28 insect populations. Of these, several were derived from laboratory studies. Using non-linear least-squares methods to estimate parameters from a modified Ricker model for population growth (Hassell, 1975), it was demonstrated that most insect populations were predicted to show stable dynamics. As a test of this model, Hassell *et al.* (1976a) used data from laboratory populations of *Callosobruchus chinensis* showing monotonic, damped oscillations, or two-point limit cycles to validate their predictions. Both the monotonic and damped populations appeared in the appropriate regions of a stability plane while the cycling population was on the margins of the appropriate stability zone. More interestingly, by using Nicholson's blowfly data, Hassell *et al.* (1976a) predicted that the model parameters for this population should show chaotic (seemingly random) population fluctuations.

## C. Chaos

Chaos is a phenomenon that has attracted a wealth of interest in population ecology (May, 1974; Schaffer, 1984; Hastings *et al.*, 1993). Biologists have shown that the strong non-linear negative feedback (due to density-dependent processes) in ecological populations have the potential to generate chaotic (apparently random) dynamics. For example, in a number of theoretical models it has been demonstrated that single populations show seemingly chaotic dynamics (May, 1974, 1976; May and Oster, 1976).

Laboratory experiments have been truly instrumental in shaping our understanding of these non-linear processes. Analysis of Nicholson's blowfly data has been worked and re-worked as a test of chaotic or limit-cycle dynamics (May, 1973; Gurney *et al.*, 1980; Ellner and Turchin, 1995). Currently, with the availability of a range of non-linear statistical techniques, most laboratory populations have been shown not to have chaotic dynamics (Ellner and Turchin, 1995). However, the dynamics of Nicholson's blowflies remain a moot point: a realistic population model of these dynamics has a positive Lyapunov exponent (a statistic that asks whether in the long run two initially nearby points converge or diverge). This is indicative of chaotic dynamics (Ellner and Turchin, 1995). These dynamics of *L. cuprina* first studied by Nicholson to investigate the nature of equilibrium dynamics and regulation remain a focus of contemporary research in non-linear population dynamics.

More extensive laboratory experiments have been undertaken to explore the nature of non-linear dynamics and chaos using *Tribolium castaneum*. Desharnais, Costantino, Dennis, and colleagues have explored the non-linear dynamics of these *Tribolium* populations (Desharnais and Liu, 1987; Costantino *et al.*, 1995, 1997; Dennis *et al.*, 1995, 2001) by developing a single theoretical model of the age-structured beetle populations, using robust statistical analogs of this model and long-term laboratory experiments. By manipulating key demographic processes (e.g., adult survival) of the beetles (predicted to change the population dynamics from analysis of the age-structured model), the dynamics of *Tribolium* were monitored. In an initial series of replicated experiments, manipulation of adult death rate changed the population dynamics from stable dynamics to periodic cycles (Costantino *et al.*, 1995). In a further set of replicated experiments, increments in adult recruitment were shown to shift the dynamics of the populations from equilibrium to cycles to chaos (Costantino *et al.*, 1997). Based on the initial approach, Hassell *et al.* (1976a) and more recent developments of fitting single models to ecological data (Turchin and Taylor, 1992; Dennis and Taper, 1994; Dennis *et al.*, 1995, 2001), there remains the potential for extending the rationale of model choice, fitting, and selection to understanding the dynamics of density-dependent feedback for a range of species under different ecological scenarios.

## D. Competition

### 1. Interspecific Competition

Originally formulated as a theoretical problem (Lokta, 1925; Volterra, 1926), the central ideas of interspecific competition have principally been shaped by laboratory experiments. The effects of interspecific competition

were first illustrated by Gause (1933) who used yeast cells. It is clear that Gause chose the confines of the laboratory to focus on the ecological nature of the interaction between competitors in a controlled environment. In a series of controlled experiments using yeast cell populations (*Saccharomyces cerevisiae* and *Schizosaccharomyces kephir*), Gause investigated the mechanisms of both intra- and interspecific competition by combining a series of theoretical ideas (logistic population growth, Lotka-Volterra competition) with a set of carefully designed experiments. By estimating the coefficients of interspecific competition between *S. cerevisiae* and *S. kephir*, Gause demonstrated that the effects of interspecific competition can, as theory predicted, inhibit the population growth of the two species. Further, from these experiments, it was shown that the effects of interspecific competition is remarkably asymmetric: *S. kephir* has much more of a dramatic effect on the growth of *S. cerevisiae* than the reciprocal effect. In fact, *S. kephir* decreases the opportunity for growth of *S. cerevisiae* by a factor of three. This phenomenon of asymmetries in competitive interactions has wide appeal and has been observed in a number of additional laboratory and field experiments (Lawton and Hassell, 1981) and, more recently, has been extended to more complex species interactions (Chapin and Bonsall, 2000).

In a separate series of experiments, Gause extended these ideas of interspecific competition using Protozoa. In particular, experiments were designed to mimic the renewal of energy in a competitive system. Although experiments on Protozoa had preceded Gause's work (e.g., Woodruff, 1914; Eddy, 1928), by designing carefully controlled experiments, Gause was to bring rigor to experimental population ecology by reducing a system to a number of understandable components. First, Gause corroborated that the logistic growth patterns also underpinned the population growth of the Protozoa populations. Second, the effects of interspecific competition were clearly demonstrated in a system where the energy inputs were carefully controlled. Finally, the amount of energy obtained by each species was evaluated and used to predict the outcome of the competitive interaction. From these experiments, theories have been developed and extended into the quantitative rules and predictions on the outcome of competition, such as the competitive exclusion hypothesis (Hardin, 1960) and energy utilization ( $R^*$ ) rules (Tilman, 1982, 1988).

Using a similar series of laboratory experiments, Park (1948) demonstrated that the effects of interspecific competition can be manifest in flour beetle (*Tribolium*) cultures. Using cultures of *Tribolium castaneum* and *Tribolium confusum* the population dynamics of single and interspecific competitive interactions were studied over a four-year period. Single-species populations established equilibrium densities for the duration of the study. In competition, one of the species of *Tribolium* was driven to extinction. Typically, *T. confusum* was lost from the interaction. Park demonstrated

that the outcome of competition can also be mediated by the effects of a non-discriminant parasite. In the presence of the microsporidia, *Adelina tribolii*, the outcome of the competitive interaction was switched and typically *T. castaneum* was driven to extinction. This effect of a third species on two potential competitors is a class of indirect interactions that involves the population dynamics of multiple species.

## 2. Apparent Competition

More specifically, the class of indirect interactions in which two species that do not compete for resources share a common natural enemy is known as apparent competition. Theoretically, it is known that this indirect interaction can lead to the loss of one species due to the numerical and functional response of the natural enemy. For example, consider the consequences of the invasion of a second prey species into an established predator-prey interaction. The availability of alternative prey in the diet of a predator leads to an increase in the size of the predator population. With a larger predator population there is potential for more attacks on both prey species and if sustained over time, the species that suffers the higher number of attacks or has the lower growth rate is eliminated. The natural enemy is then a dynamic monophage (Holt and Lawton, 1993): through the dynamical interaction with its prey, the predator persists with a single prey due to the consequences of apparent competition. Although the theoretical consequences of apparent competition are relatively well-established (Holt, 1977, 1984; Holt and Lawton, 1993, 1994; Bonsall, 2003; Bonsall and Holt, 2003), recent laboratory experiments have demonstrated that apparent competition has the potential to shape the structure of multispecies predator-prey interactions.

Although the single-generation cohort effects of apparent competition have been largely understood in predator-prey systems through laboratory and field observations (Holt and Lawton, 1994), only relatively recently have laboratory experiments taken a more central role and been used to explore the long-term transgenerational effects of apparent competition. Using a laboratory system of a simple insect host-parasitoid assemblage (*Plodia interpunctella*, *Ephestia kuehniella*, *Venturia canescens*), Bonsall and Hassell (1997, 1998) demonstrated that the parasitoid, *V. canescens* can induce apparent competition between two of its hosts (*Plodia* and *Ephestia*). Replicated time series were established in which the separate pairwise predator-prey interactions (*P. interpunctella*-*V. canescens* and *E. kuehniella*-*V. canescens*) were shown to always persist. Time series analysis revealed that the dynamics of these pairwise interactions were described by simple linear statistical models (Bonsall and Hassell, 1998). The full three-species interaction, in

which the two hosts were not allowed to compete for resources and parasitoid foraging on both species was not restricted, did not persist. *E. kuehniella* was always lost from the interaction and *V. canescens* became a dynamic monophage through its population dynamic actions on the availability of multiple prey. Although the empirical tests of competition and apparent competition have been motivated by theory, testing contrasting concepts for these patterns remains a challenge for this area of ecology.

## E. Predation

Initially our understanding of the components of predation were shaped by the theoretical models of Lokta (1925), Volterra (1926), Nicholson and Bailey (1935), and Thompson (1924). In testing the ideas that predation can lead to oscillatory or diverging dynamics, the use and application of controlled environment experiments or observations have been exceptionally influential. Nicholson and Bailey (1935) illustrated theoretically that the interaction between an exponentially growing host and a randomly searching parasitoid leads to non-persistent, diverging dynamics due to overexploitation of the host by the natural enemy. Several empirical studies have confirmed that this combination of factors can lead to extinction of predators and/or prey (Burnett, 1958; Huffaker, 1958; May *et al.*, 1974; Bonsall *et al.*, 2002). Understanding the ecological factors that allow predator-prey interactions to persist has been a dominant area of ecological research utilizing a wide range of models and model systems (e.g., Hassell, 1978, 2002; Murdoch *et al.*, 2003a).

### 1. Components of Predation

One of the fundamental components of predation is the functional response. This is the relationship between the number of prey attacked and prey density (Solomon, 1949). For the three types of functional response (linear, asymptotic, sigmoid) laboratory experiments have had an influential role in determining how these responses affect the population dynamics of predator-prey interactions. In particular, in a series of experiments and model analysis, Lawton and colleagues explored how the components of arthropod predation are shaped by the prey death rate, the effects of prey density on predator development and survival, and the effects of prey density on predator fecundity (Lawton *et al.*, 1975; Beddington *et al.*, 1976; Hassell *et al.*, 1976b). In a similar vein, laboratory experiments have been used to explore the detailed foraging activities of insect predators. In particular,

Cook and Hubbard (1977) examined how insect parasitoids might be expected to forage optimally for hosts. They predicted that the expected rate of prey an insect predator will encounter in a patchy environment should be reduced to the same level in all patches. By developing an optimal foraging model they showed that the search strategy for *Nemeritis* (*Venturia*) *canescens* should alter as the density of the parasitic wasp is changed. In an earlier set of experiments, Hassell and Varley (1969) had shown that the behavior of insect predators and in particular parasitic wasps can be clearly influenced by the presence of conspecifics. As predators aggregate around patches of high prey density it is increasingly likely that they will interact while searching for prey. Such an effect has been termed 'mutual interference' and has been observed in the behavior of a number of predators such as *Diaeretiella rapae* (Hassell, 1978), *Trybliographa rapae* (Visser *et al.*, 1999), *Nemeritis canescens* (Hassell, 1971), and *Typhlodromus longipilus* (Kuchlein, 1966). The generic effect of mutual interference is to reduce the available search time in direct proportion to the frequency of encounters. However, not all search behaviors by predators in the presence of patchily distributed prey can be ascribed to mutual interference. Free *et al.* (1977) argued that aggregation of predators to patchily distributed prey can lead to a phenomenon known as 'pseudointerference'. Pseudointerference arises due to the differential exploitation of host patches. Initial aggregation to high-density patches is profitable as a higher proportion of hosts are attacked than would be expected under a random search strategy. However, such behavioral tendencies introduce a density-dependent reduction in searching efficiency that causes an apparent interference relationship. This is now known as pseudointerference. Although a number of empirical studies have highlighted the different role of behavioral interference (Visser *et al.*, 1999), interference is essentially the phenomenon of optimal foraging (Charnov, 1976) extended to predator-prey interactions (Cook and Hubbard, 1977) but with a more direct connection to the role of spatial heterogeneity in predator-prey interactions.

## 2. Spatial Heterogeneity

The effect of heterogeneity where some individuals are more at risk of attack than others is predominant in predator-prey interactions. Heterogeneity can be manifest at a number of different levels such as at the individual level through physiological or genetic differences, at the population level through differences in the local spatial distribution of prey or at the community level by the availability of different prey or habitats. Nevertheless, it is the role of spatial heterogeneity (patchily distributed prey within a habitat) that has attracted considerable attention, and laboratory experiments have been



instrumental in shaping our understanding of the role of this ecological process on the persistence of predator-prey interactions.

Most influential in the study of spatial heterogeneity has been the work on host-parasitoid interactions (Bailey *et al.*, 1962; Hassell and May, 1973, 1974; May, 1978). These early theoretical models demonstrated that aggregation by parasitoids to patches of high-host density was potentially a major contributing factor to the temporal stability of the interaction. More recently this has been re-examined in terms of heterogeneity in the distribution of parasitism which, if sufficient, can be strongly stabilizing (Chesson and Murdoch, 1986; Pacala *et al.*, 1990; Hassell *et al.*, 1991a). Such variability in parasitism can arise through behavioral responses by the parasitoid to host density (positively or negatively dependent on host density) or responses unrelated to host density (host density-independent). This variability gives rise to (positive, negative, or independent) spatial patterns of parasitism. It has been argued that these spatial patterns of parasitism are indicative of the temporal stability of the predator-prey interaction (Hassell and May, 1973, 1974); however, rather than the precise pattern, it is the distribution and risk of parasitism between host patches that is more influential in determining the stability and persistence of the predator-prey interaction (Pacala and Hassell, 1991; Hassell *et al.*, 1991a).

Many empirical studies have sought to identify the role of these spatial patterns of parasitism. Of the studies listed in the reviews by Lessells (1985), Stiling (1987), Walde and Murdoch (1988), and Hassell and Pacala (1990), 29% show positive (direct) density-dependent patterns of parasitism, 26% show inverse patterns, and 45% show patterns of parasitism uncorrelated with host density. Discussions on how these patterns might arise has focused on the role of the functional response (Hassell, 1982), parasitoid biology (Lessells, 1985), and the spatial scale of the interaction (Heads and Lawton, 1983). Originally highlighted by Reeve *et al.* (1989) and more recently explored by Gross and Ives (1999), inferring temporal stability from spatial patterns of parasitism is complicated by a number of difficulties, including the way parasitism is distributed within and between patches (Gross and Ives, 1999). A more robust way to test the ideas of spatial heterogeneity on the persistence of host-parasitoid interactions is to examine the population-dynamic consequences of heterogeneity from a series of well-replicated laboratory experiments. Here, we present evidence for the role of spatial heterogeneity on the population-dynamic interaction between *Drosophila ananassae* and its parasitic wasp *Leptopilina victorae*.

In particular, we contrast two different types of patchy environments: resource patches that are equally available for fly and wasp oviposition and resource patches that provide a refuge for the fly from wasp oviposition. Replicated population dynamics of these two different host-parasitoid interactions are illustrated in Figs. 2 and 3. For these population-level data,

ecological models describing the predator-prey interaction between *D. ananassae* and *L. victorae* were contrasted (Table 2). In these patchy resource systems, the most appropriate description for the dynamics of the host-parasitoid interaction in both environments is a model incorporating density dependence acting on the parasitoid:

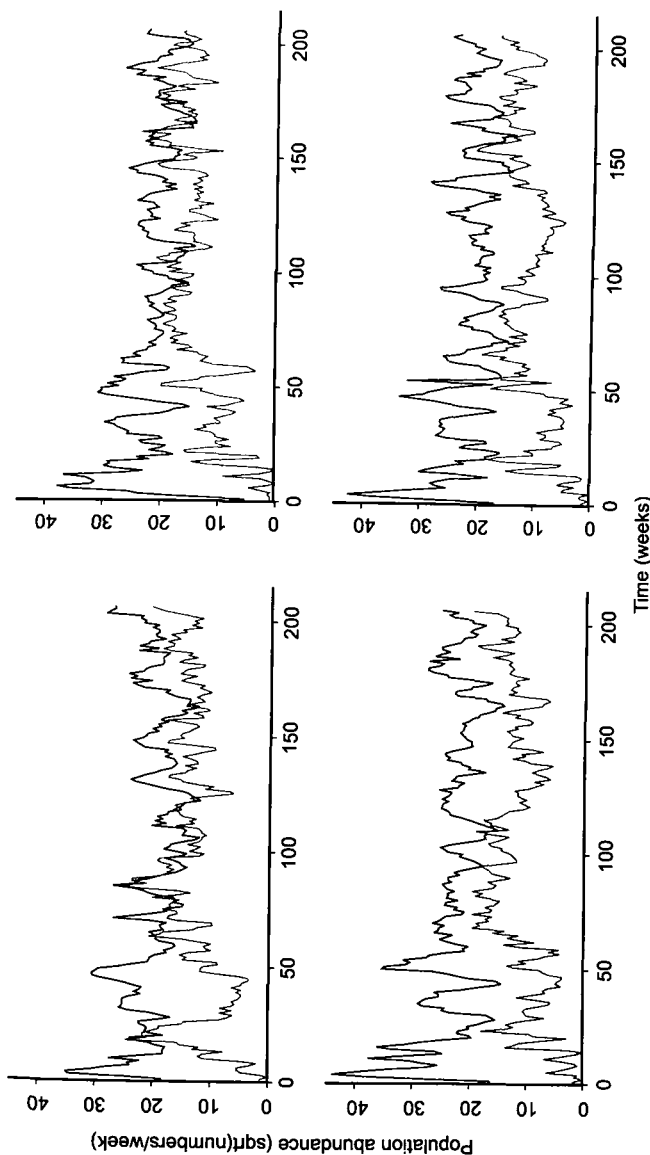
$$\frac{dH}{dt} = r \cdot H_t - k \cdot \log \left[ 1 + \frac{\alpha \cdot P_t}{k} \right] \cdot H_t \quad (7)$$

$$\frac{dP}{dt} = k \cdot \log \left[ 1 + \frac{\alpha \cdot P_t}{k} \right] \cdot H_t - d \cdot P_t \quad (8)$$

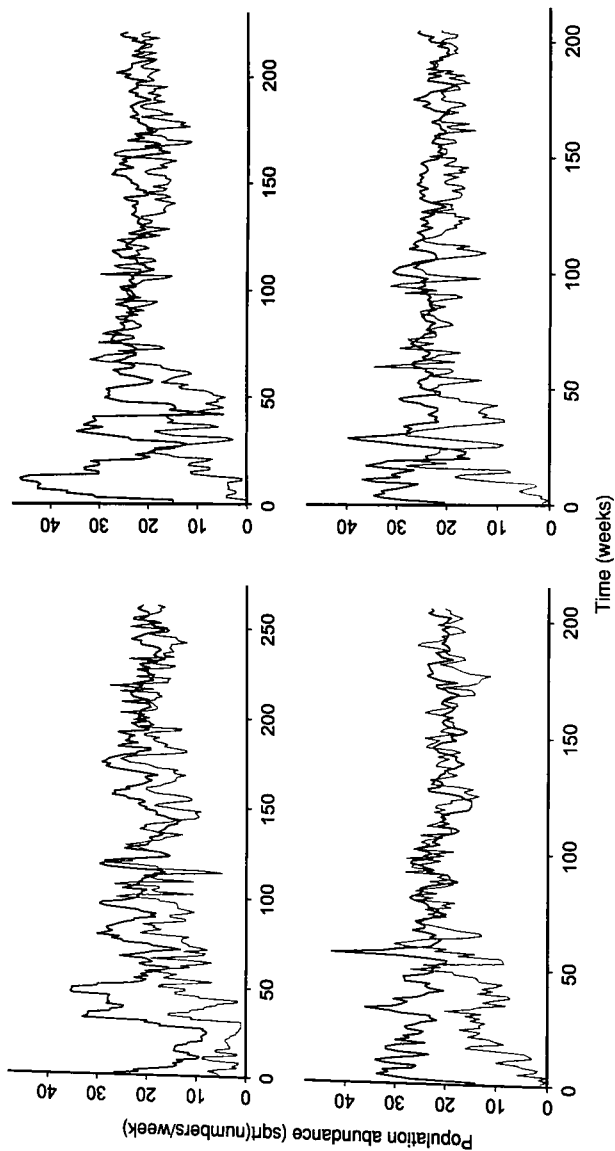
where  $r$  is the intrinsic rate of increase of the host population ( $H$ ),  $k$  is a measure of the dependence of parasitoid efficiency on parasitoid density such that as  $k$  gets smaller, the magnitude of the density-dependent effect increases,  $\alpha$  is the parasitoid attack rate, and  $d$  is the parasitoid ( $P$ ) death rate. This form of parasitism introduces density dependence to the population interaction through the processes of pseudointerference and allows persistence of the host-parasitoid interaction. In the no-refuge treatment, parameter values for the dynamics (Fig. 2), and in particular, the strength of parasitoid density dependence predicts that the dynamics of the interaction will be unstable ( $k = 4.31$ , 95% CI = 0.095). In contrast, in the refuge treatment, the dynamics are predicted to be stable since  $k < 1$  (May, 1978; Hassell, 2000) ( $k = 0.622$ , 95% CI = 0.0004) (Fig. 3).

### 3. Predator-Prey Metapopulations

The role of space and spatial dynamics are central to the patterns of the distribution and abundance of species. Although the explicit inclusion of space into population ecological theory is a relatively recent development (Gilpin and Hanski, 1991; Hanski and Gilpin, 1997), a number of early studies postulated that space might affect the persistence of ecological systems (Nicholson and Bailey, 1935; Wright, 1940; Andrewartha and Birch, 1954). That extinction-prone species interactions can persist as a result of metapopulation processes has been frequently demonstrated in models (Allen, 1975; Hassell *et al.*, 1991b, 1994; Comins and Hassell, 1996; Bonsall and Hassell, 2000). However, only rarely has this effect of increased persistence due to spatial processes been observed in experimental microcosms (Huffaker, 1958; Holyoak and Lawler, 1996; Ellner *et al.*, 2001; Bonsall *et al.*, 2002) or in the field (Hanski, 1999).



**Figure 2** Population dynamics of *Drosophila ananassae* and *Leptopilina victorae* in a patchy environment. In chronological order, 4 resource patches (apple-based media) out of 20 were renewed each week. Dynamics show that in the presence of the parasitoid, the abundance of *D. ananassae* is reduced to approximately 490 flies per week. The dynamics of the predator-prey interaction in the absence of a host refuge are expected to be unstable (model parameter estimates (with 95% CI)  $r = 1.27(0.001)$ ,  $\alpha = 0.008(0.001)$ ,  $k = 4.405(0.095)$ ,  $d = 0.746(0.003)$ ).



**Figure 3** Population dynamics of *Drosophila ananassae* and *Leptopilina victorae* in a patchy environment with a (70%) refuge for the host on all patches. In chronological order, 4 resource patches (apple-based media) out of 20 were renewed each week. Dynamics show that in the presence of the parasitoid, the abundance of *D. ananassae* is reduced to approximately 560 flies per week. The dynamics of this predator-prey interaction in the presence of a host refuge are predicted to show stable dynamics (model parameter estimates (with 95% CI)  $r = 0.371(0.0004)$ ,  $\alpha = 0.001(0.001)$ ,  $k = 0.622(0.0004)$ ,  $d = 0.864(0.001)$ ).

**Table 2** Information theoretic (AIC) criteria for three candidate models for describing the overall predator-prey dynamics between *Drosophila ananassae* and *Leptopilina victorae* in two different patchy environments (no refuges, available refuges) (all replicates pooled). Model 1 is the standard Lotka-Volterra model of the form  $\frac{dx}{dt} = rx - \alpha xy$ ;  $\frac{dy}{dt} = c\alpha xy - dy$ . Model 2 is a Lotka-Volterra model incorporating a type II functional response ( $\frac{dx}{dt} = rx - \frac{\alpha xy}{1+\beta x}$ ;  $\frac{dy}{dt} = \frac{c\alpha xy}{1+\beta x} - dy$ ). Model 3 is a Lotka-Volterra model replacing the type II functional response by an expression for density dependence acting on the parasitoid ( $k \cdot \log[1 + \frac{\alpha y}{k}]$ ) (May, 1978). Models were fitted using a bivariate Gaussian likelihood to time series data. Comparison of the models for the dynamics of *D. ananassae* and *L. victorae* in two different environments (refuges, no refuges) reveals that the most parsimonious description is the model incorporating parasitoid density dependence (Model 3)

### Host-parasitoid Interaction

	No refuges	Refuges available
Model 1	23,302.442	28,406.886
Model 2	23,342,220	26,430.148
Model 3	21,316.096	24,437.878

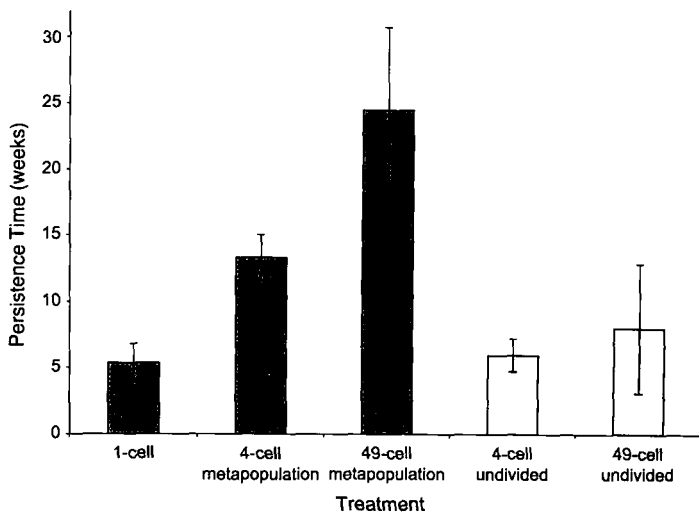
In a classic series of experiments, Huffaker (1958; Huffaker and Kennet, 1956; Huffaker *et al.*, 1963) investigated the effects of spatial structure on a laboratory mite predator-prey interaction. Huffaker designed a suite of experiments using oranges as patches in various arrangements (fully exposed oranges, partially exposed oranges) to test ideas of the effects of spatial structure on the persistence of predator-prey interactions. First, Huffaker (1958) showed that the predator-prey interaction could not survive in a homogenous environment without dispersal. Second, to test the role of migration, Huffaker elegantly manipulated the spatial environment (wooden posts to aid dispersal, petroleum jelly to restrict dispersal) and demonstrated an increased persistence time for the system. Finally, in an extension to this work, the experimental system was expanded to include more patches and more environmental complexity (Huffaker *et al.*, 1963). From this series of experiments Huffaker and colleagues showed that increased persistence of the predator-prey interaction was a consequence of the spatial structure and complexity of the system. In a similar series of experiments, Pimental *et al.*, (1963) showed that the persistence of the interaction between *Musca domestica* and *Nasonia vitripennis* and *Lucilia sericata* and *Nasonia vitripennis* could be enhanced by linking patches by dispersal (via tubes). In a series of population-level experiments, it was observed that when host densities were low, wasp dispersal increased. However, when parasitoid dispersal was restricted (via baffles covering the dispersal tubes), persistence time was increased. In contrast to the conceptual predictions of both Andrewartha and Birch (1954) and Nicholson and Bailey (1935), as dispersal of the natural enemy was

reduced, the densities of both the wasp and its host increased and the amplitude of the predator-prey fluctuations declined. Pimental *et al.* (1963) argued that the original Nicholson-Bailey model was predicted to capture predator-prey dynamics in simple systems and that their designed laboratory systems may not be simple due to the inclusion of dispersal and baffles.

Recently, the role of metapopulation structures on the persistence of predator-prey interactions have been more extensively tested using laboratory systems (Holyoak and Lawler, 1996; Ellner *et al.*, 2001; Bonsall *et al.*, 2002). Theoretical models predict that non-persistent predator-prey interactions may persist due to the effects of limited dispersal (Hassell *et al.*, 1991b; Comins *et al.*, 1992). The emerging consensus from a series of laboratory experiments on a wide range of organisms is that limited dispersal clearly has a major influence on the persistence of populations. For example, recent work on the interaction between the bruchid beetle *Callosobruchus chinensis* and its parasitic wasp *Anisopteromalus calandrae* has shown that persistence of this extinction-prone host-parasitoid interaction is enhanced by a metapopulation structure (Bonsall *et al.*, 2002). Through a series of replicated experiments the persistence of host-parasitoid interactions in metapopulations with limited and unlimited dispersal was explored. By controlling for the effects of any increased persistence due to the effects of the availability of more resource in the system, persistence of this host-parasitoid interaction was shown to be principally driven by coupling habitats with limited dispersal (Fig. 4). In comparison to other studies on predator-prey metapopulation dynamics, Bonsall *et al.* (2002) demonstrated that spatial structure has a primary influence on the persistence of trophic interactions. However, in a series of controlled experiments using a mite system (*Tetranychus urticae*-*Phytoseiulus persimilis*), Ellner *et al.* (2001) have shown that habitat structure per se has a limited role in the persistence of a predator-prey metapopulation and it is the reduced probability of attack by the predator that allows the system to persist. These two examples show that by using replicated, designed experiments, laboratory systems permit a number of models on spatial dynamics and persistence of predator-prey metapopulations to be evaluated. For instance, it is now feasible, using the *C. chinensis*-*A. calandrae* system to explore how the effects of local patch processes (demographic stochasticity) affect the regional dynamics of metapopulations (Bonsall and Hastings, 2004).

## F. Stability and Complexity in Ecosystems

The stability-complexity debate was initially sparked by the question whether assemblages with more species are more or less persistent than species-poor assemblages (Elton, 1958; May 1971, 1973). The debate was initially



**Figure 4** Predator-prey persistence times in two different metapopulation environments (4-cell, 49-cell systems). Persistence time for the interaction between *Callosobruchus chinensis*-*Anisopteromalus calandrace* increases as the metapopulation size increases. This is due to the effects of limited dispersal (barriers to dispersal open for 2 hours each week) rather than the increased availability of resources in the metapopulations (Bonsall *et al.*, 2002).

focused on the population dynamics of assemblages, and theoretical models predicted that assemblages with more species may not be more stable (in the strict population dynamic sense) than assemblages with fewer species. In particular, May (1973) showed, theoretically, that multispecies communities in which the individual populations of each species are stable could be unstable if the food-web is highly connected or the average interaction strength is too large. That is, from an assessment of the local stability of a community of  $n$  species, the system is stable if:

$$s(nC)^{1/2} < 1, \quad (9)$$

where  $s$  is the average interaction strength and  $C$  is the connectance of the food-web. More recently, McCann *et al.* (1998) have corroborated May's (1971, 1973) findings by showing that weak links allow the persistence of simple three and four species assemblages. This general result that complexity does not necessarily beget stability has been tempered by discussion on the definitions of 'stable' and 'persistent' (Pimm, 1984), the role of energy flow through ecosystems (Pimm and Lawton, 1977), and more recently on the role of ecosystem function and services (e.g., decomposition, facilitation) provided by species in communities (Kinzig *et al.*, 2002).

While the theory surrounding this concept is well developed, laboratory experiments on the stability-complexity debate have only recently been undertaken. For instance, Fox and McGrady-Steed (2002) tested the prediction that species connected randomly by strong interactions are unlikely to exhibit stable, feasible equilibria using experimental communities of bacteria, protists, and small metazoans. Analysis of long-term data from experimental communities that varied initially in species richness ( $n$ ), connectance ( $C$ ), and composition showed that the probability of stability declined with complexity. Moreover, Fox and McGrady-Steed (2002) demonstrated that communities converged in connectance over time so that the fraction of interspecific interactions was independent of species richness. In a similar series of replicated microcosm experiments, Weatherby *et al.* (1998) established 63 different microcosms from a pool of six protist species (three bacterivores, two predators and one omnivore). Forty-seven of these showed a repeatable collapse to one of eight communities, and persistent communities could be reached from several different starting communities. In a more detailed study of the effects of species richness, Lawler (1993) tested the hypothesis that the degree of species richness affected the persistence, abundance and temporal variability of protist communities. In general, species food-web composition affects the persistence and mean abundance of several species: species abundance declines in species-rich food-webs and temporal variability is increased as the number of predator-prey pairs increases.

Laboratory microcosms, and in particular the use of aquatic communities have been exceedingly beneficial to our understanding of and in prediction of the effects of food-web architecture on population dynamics (Lawler and Morin, 1993; Morin and Lawler, 1995), the effects of multispecies competition on community composition and resource utilization (Neill, 1975), the effects of diversity on ecosystem function (McGrady-Steed *et al.*, 1997), the effects of productivity on food-chain dynamics (Kaunzinger and Morin, 1998, Fukami and Morin, 2003), and the effects of environmental warming on food-web structure and ecosystem function (Petchey *et al.*, 1999). However, it is the effects of species diversity on ecosystem function that has attracted the most recent interest. Naeem *et al.* (1994) clearly demonstrated using replicated terrestrial microcosms that the loss of biodiversity can alter the performance and function of ecosystems. By manipulating levels of biodiversity, ecosystem performance and community responses, such as respiration, decomposition, nutrient retention, plant productivity, and water retention, are affected. More recently, based on the findings from these controlled microcosm experiments the effects of species diversity on ecosystem performance has been extended to field studies (Hector *et al.*, 1999). However, there remains little rigorous comparison of models of community dynamics with experimental data. With the availability of a diverse wealth of community biology theories (e.g., Morin, 1999; Tokeshi, 1999), it is appropriate to integrate more fully



ecological experiments on community and ecosystem dynamics with the theoretical developments in this area of ecology.

#### IV. FUTURE PERSPECTIVES

Our principal argument for the rationale for the use of laboratory microcosms is to move away from simple significance tests towards a more pluralistic approach to understanding ecological processes and mechanisms. Selecting an a priori set of candidate models, computing a criterion based on information loss for each of these possible models, and accepting the one that minimized the information loss for the ecological problem remains a simple and compelling concept. Such an approach has formal, theoretical roots in information theory and provides a powerful alternative to the conventional approach to ecological research. With the availability of theoretical ecological models, this rationale coupled with laboratory experiments is appealing and holds the hope of some exciting developments in ecology.

A number of broad ecological problems still necessitate the design and implementation of laboratory microcosms. While by no means complete, this list includes the use of laboratory experiments to understand space, noise, transient dynamics, and the rules of species assembly. In this final section, we highlight five areas where laboratory experimental microcosms are likely to have an important impact on our understanding of the underlying ecological principles.

##### A. Population Dynamics

One of the obvious ways that laboratory experiments can be integrated with the rationale of model choice is through an analysis of the time series of the population dynamics of species interactions. While time series are observational and often inference of mechanism from such data is difficult (Ellner *et al.*, 1997), identifying the ecological mechanism from ecological population data is a direct application of the rationale of model selection and choice. While previous studies have highlighted the integration of mechanistic models and time series analysis to interpreting population-level phenomena such as cyclic dynamics (e.g., Kendall *et al.*, 1999) or the dynamics of specific systems (Dennis *et al.*, 1995, 2001), a fuller approach to testing candidate models and assessing contrasting ecological effects remains a straightforward but novel approach to problems on the dynamics of populations. For example, recent findings have highlighted that the population dynamics of generalist consumers can be described by simple single-species models (Murdoch *et al.*, 2002). This result was obtained from 112 time series from a variety of sources. That multispecies interactions can

be collapsed to single-species interactions is appealing but not without controversy (Rohani *et al.*, 2003; Murdoch *et al.*, 2003b). However, a set of manipulative experiments could be designed to test this idea. Generalist natural enemies such as some parasitic wasps are readily cultured and multispecies laboratory systems are clearly amenable to resolving this problem through the testing and comparison of competing single and multispecies models. Moreover, the maxim that mechanism cannot be inferred from population time series is now in doubt (Table 1). The combination of laboratory experiments and appropriate model choice holds the possibility that mechanistic understanding can be gained from ecological time series.

## B. Role of Productivity in Ecosystems

While laboratory experiments may not be appropriate for testing ecosystem responses to perturbations, such microcosm experiments can be used successfully in testing specific ecosystem processes. One such process that warrants further study is the role of productivity. Productivity is the amount of locally available energy to a particular ecosystem and is known, theoretically, to influence species diversity (Rosenzweig and MacArthur, 1963), predator-prey interactions (Rosenzweig, 1971), and more complex multispecies assemblages (Diehl and Feissel, 2000; Bonsall and Holt, 2003). While the theory surrounding the role of productivity on species interactions is well-established and the broad pattern of the relationship between species diversity and productivity is widely documented (e.g., Tilman and Pacala, 1993), empirical support for the ecological effects (model parameters) remains relatively scarce. Models of productivity are known to take a variety of contrasting forms (Waide *et al.*, 1999) and comparing models that describe monotonic relationships ( $diversity = m_1 \cdot productivity + c$ ), humped relationships ( $diversity = m_1 \cdot productivity + m_2 \cdot productivity^2 + c$ ), or more general (non-parametric) relationships ( $diversity = f(productivity) + c$ ) between productivity and diversity would allow temporally consistent patterns between different species interactions to be explored. There is clearly a scope for developing robust, well-replicated laboratory microcosm experiments to contrast a range of concepts (models) on the role of ecosystem productivity on species diversity and interactions.

## C. Role of Weak Links in Ecosystems

Theoretical models have indicated that multispecies interactions with strong interaction strengths are not compatible with the persistence of speciose and diverse food-webs (May, 1971; McCann *et al.*, 1998). While this has been the

focus of considerable attention (Pimm, 1982; King and Pimm, 1983; Pimm, 1984), several testable predictions remain unanswered. These include: Do weak interactions predominant in persisting multispecies assemblages? Are species-poor food-webs more likely to show oscillatory dynamics compared to more species-diverse food-webs? What is the relative effect of more strong interactions over weak interactions on multispecies dynamics? Understanding how these different rules of assembly affect the dynamics and persistence of multispecies interactions rests on an appropriate measure of species interaction strengths (the magnitude of one species on another) (Laska and Wootton, 1998). While several measures of interaction exist such as estimates based on the community matrix (Levins, 1968), the Jacobian matrix (May, 1973), the inverted Jacobian matrix (Bender *et al.*, 1984), per capita effects (Paine, 1992), or population-dynamic effects (Laska and Wootton, 1998), ecological interaction strengths are traditionally thought to be indeterminate in their response to changes in biotic or abiotic perturbations (Bender *et al.*, 1984). Recent work has highlighted that the species interactions are contingent, stochastic, and non-linear (Bonsall *et al.*, 2003). Species interactions may be misinterpreted for reasons associated with experimental design (Bender *et al.*, 1984) or non-linear effects (Bonsall *et al.*, 2003). However, it remains an attainable goal that a progressive understanding of species interaction strengths and their impact on multispecies assemblages can be achieved. Given that species interactions can be manipulated in laboratory experiments (through press or perturbation responses) and that complex food-webs can be constructed from community modules (Holt, 1997), the use of laboratory microcosms in understanding interaction strength effects holds the hope of exciting advancements in community ecology.

#### **D. Role of Noise in Ecological Interactions**

Although the effects of environmental noise and climatic variability (e.g., NAO, ENSO) on the dynamics of populations have been explored (Grenfell *et al.*, 1998; Pascual *et al.*, 2000), the effects of stochasticity on single and multispecies population dynamics still remain difficult to evaluate. For instance, it is not obvious whether stochasticity acts in an additive or multiplicative fashion to influence the dynamics of species interactions. That is, does noise just simply have a scaling effect on dynamics or is it that noise interacts with endogenous processes to induce qualitatively different dynamics? Theoretical models predict that noise can influence the dynamics in a more multiplicative way (Petchey *et al.*, 1997; Greenman and Benton, 2003). However, experimental tests of the effects of environmental and/or demographic stochasticity remain relatively rare (however, see

Petchey *et al.*, 1999, and Benton *et al.*, 2002). Parameter optimization and model selection requires a decision about the underlying noise processes (e.g., environmental or demographic), and laboratory experiments are well suited to testing the effects of noise on the dynamics (e.g., Dennis *et al.*, 2001). Manipulating environmental conditions have been shown to affect population dynamics (Beckerman *et al.*, 2002). However, contrasting different noise terms and differentiating between the additive and multiplicative effects of noise remains an area for future development. Extending our understanding of the effects of noise on multispecies interaction also remains unclear and understanding the population dynamic consequences through the use of laboratory systems and model choice remains a challenge for population ecological research.

### **E. Role of Space in Ecological Interactions**

One of the most frequently raised questions in ecology is how do space and spatial processes affect species interactions. While the principle of space has been widely acknowledged (Nicholson and Bailey, 1935; Wright, 1940; Skellam, 1951; Andrewartha and Birch, 1954) and is fundamental to the understanding of the distribution and the abundance of species, experimental tests of spatial processes remain scarce. In particular, the concept of the metapopulation has become the central paradigm in spatial ecology (Hanski, 1999). However, designing well-replicated, spatially-explicit and spatially-relevant experiments in the field remains difficult if not impossible. The use of laboratory studies in understanding spatial processes is clearly of benefit. The original experiments by Huffaker (Huffaker *et al.*, 1963) and Pimental (Pimental *et al.*, 1963) highlighted how laboratory systems can be developed to tackle research problems on spatial ecology. More recently, laboratory microcosms examining metapopulation processes have been developed (Holyoak and Lawler, 1996; Bonsall *et al.*, 2002). However, several research problems that remain unanswered such as the effects of more complex habitat arrangements, the role of source-sink dynamics, and the existence of between-patch heterogeneity are all potential issues that impinge on our understanding of spatial dynamics. These can be realistically examined with designed laboratory experiments. Moreover, process- and individual-based models on metapopulation dynamics and interactions abound in the literature (Allen, 1975; Hassell *et al.*, 1991b; DeAngelis and Gross, 1992; Durrett and Levin, 1994), and within our framework of model choice and selection, the comparison of different spatial concepts on the dynamics and persistence of ecological systems remains an exciting area for development.

## V. CONCLUSIONS

We have argued that laboratory microcosm experiments have had a predominant role in conceptualizing ideas in ecology. If the aim in ecology is to find laws and axioms, then laboratory experiments will remain a valuable approach for collating evidence on ecological patterns and processes underpinning the distribution and abundance of organisms. In short, the detailed history of natural communities is seldom known and, therefore, it is often difficult to deduce the ecological patterns or mechanisms. To this end, laboratory experiments will remain essential for exploring the structure and function of ecological assemblages.

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