

EXPERIMENTAL ECOLOGY

Issues and Perspectives

Edited by

William J. Reisetarits Jr.

Joseph Bernardo

New York Oxford

Oxford University Press

1998

The Motivation for and Context of Experiments in Ecology

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Over the past three decades, experimentation in ecology has become increasingly common (Connell 1972, 1983; Paine 1977; Schoener 1983; Hairston 1989). The experimental method has provided ecologists with a technique for examining the origins of pattern and the role of various processes in natural systems. As experimentation has proliferated in ecology, specific prescriptions for the design and implementation of experiments have emerged (e.g., Bender et al. 1984, Hurlburt 1984, Underwood 1986, Hairston 1989, Underwood and Petraitis 1993, Wootton 1994b). While there is merit in prescribing rigorous requirements for the design of experiments, it should not be carried out so as to limit the range of possible experimental approaches that can be usefully applied. For this reason, it is helpful to keep in mind the varied uses of experiments in ecology. In this chapter, we examine what we consider to be the three primary motivations for the use of experiments in ecology, illustrating them with examples drawn both from our work and from the wider literature. We then discuss how different philosophical approaches and different questions of interest in ecology call for different types of (equally valid) experimental designs and advocate applying experiments in an integrated program of ecological study.

The Motivation for Experiments

For our purposes, we will consider an experiment to involve manipulating one or more factors in a system, while the effects of other factors are either minimized or unmanipulated. This is best done in such a way that other factors do not vary systematically with the manipulation, although occasionally it may be useful to manipulate a number of factors at once simply to introduce variation into the study system (for example, imposing disturbance to initiate a successional sequence). Laboratory experiments often hold other factors as constant as possible, while field experiments usually

allow other factors to vary naturally, employing randomization techniques to minimize the effects of confounding variables. Regardless of the type or specific goals of a given manipulation, all properly designed experiments provide unambiguous knowledge of the primary source of variation in a factor and therefore isolate the effect of that manipulated factor on the study system. Our definition of experiment follows closely that of Paine (1994), with the exception that we do consider some mensurative endeavors as experiments. We see three general reasons why experiments are conducted in ecology; we list them and discuss their contributions to ecology in the following sections.

Experiments as Means of "Seeing What Happens"

Perhaps the most common type of experiment currently conducted in ecology is one where a factor is suspected to have some effect on the system and is manipulated to see what happens (curiosity-driven experiments). For example, Paine (1966, 1974) experimentally removed the starfish *Pisaster ochraceus* from stretches of rocky shores of Washington State and compared the resulting set of sessile species to those on unmanipulated stretches of shore to "see what would happen." He found that the diversity of organisms attached to or foraging on the rock surface was reduced in the absence of starfish because a major prey of the starfish, the mussel *Mytilus californianus*, took over most of the available bare space when released from control by its predator. Likewise, Wilbur and his colleagues (e.g., Wilbur 1972, Morin 1983, Alford and Wilbur 1985, Wilbur 1987, Wilbur and Fauth 1990, Leibold and Wilbur 1992) have systematically manipulated a wide array of biological and physical factors to determine the nature of their effects in artificial pond communities. These studies have found, among other things, that size structure, phenology, the composition of predators and competitors, nutrients, and habitat permanence can all play roles in affecting community and ecosystem patterns in small ponds. In our own work, birds in rocky intertidal communities have been manipulated to determine what direct and indirect effects they might have on associated invertebrates and algae (Wootton 1992, 1993a, 1994a, 1995).

There are several benefits of conducting experiments that are motivated simply by curiosity about their outcome. First, they can sometimes generate great insight into the biological and physical processes operating in ecological systems and spawn theoretical and methodological advances in the field. For example, experimental removals of starfish (Paine 1966, 1974) yielded the idea of keystone species and have subsequently inspired a great deal of investigation into food web structure, indirect effects, and the relative strength of species interactions. Experimental explorations in the laboratory of the effects of habitat arrangements on predatory and herbivorous mites by Huffaker (1958) spawned a heightened awareness of the role that spatial structure can play in stabilizing the interactions among species. Paine and Vadas (1969) manipulated sea urchins, and their observations prompted an initial formulation of the intermediate disturbance hypothesis. In our own work, outcomes derived from manipulating intertidal birds have prompted the development of a mechanistic framework for identifying potential indirect effects (Wootton 1992, 1993a) and of statistical approaches to disentangling indirect effects (Wootton 1994a).

Second, such curiosity-driven experiments more commonly provide an increase in our understanding of a specific system that is not possible by simple observation. Often there is insufficient variation in a study system to derive insights from observational data alone, and when there is only natural variation several factors may often covary and therefore be difficult to tease apart. As more and more pieces of a given study system are uncovered through experimental manipulation, we gain a better idea of the rules under which that system operates and, consequently, what types of theory might be applied effectively to understand and predict the dynamics of the system. Toward this end, it is likely that this experimental approach will be most effective when applied to specific model systems, in much the same way that developmental biologists concentrate their experimental effort on the fruit fly *Drosophila melanogaster*, the nematode *Caenorhabditis elegans*, the sea urchins *Strongylocentrotus* spp., the zebra fish *Brachydanio rerio*, and the house mouse, *Mus musculus*. When experiments are conducted haphazardly across different systems, we are left with a partial understanding of numerous systems, no particularly complete understanding of any, and no idea of the relative importance of different species or processes. Thus, exploratory (“see what happens”) experimental work will be most effective when concentrated on several model systems of relatively high experimental tractability such as old-fields/grasslands (e.g., Tilman and Wedin 1991, Goldberg and Barton 1992), desert communities (e.g., Davidson et al. 1984, Brown and Heske 1990), benthic marine communities (e.g., Connell 1961, Paine 1966, Dayton 1971, Sutherland 1974, Menge 1976, Lubchenco 1978, Sousa 1979, Underwood et al. 1983, Pfister 1995), and freshwater communities (e.g., Wilbur 1972, 1987; Werner and Hall 1976; Morin 1983; Werner 1984; Schindler et al. 1987; Leibold 1989; Power 1990; Carpenter and Kitchell 1993; Wootton and Power 1993).

Third, “see what happens” experiments can be closely allied with important applied ecology issues. In these cases, the experiment is motivated by a conservation-related concern and is often performed at relatively small spatial and temporal scales in the hopes that the results will be concordant with those at larger scales. For example, Peterson et al. (1987) used a field experiment to examine the effects of commercial clam raking (a process that disturbs marine soft sediment habitats) on subsequent recruitment of the clam *Mercenaria mercenaria*, as well as the effect on other organisms in shallow estuarine areas. Similarly, Brosnan and Crumrine (1994) experimentally manipulated human “trampling” effects in marine rocky intertidal plots either 20 × 20 cm or 20 × 30 cm to glean insight into how tourism in coastal areas might affect intertidal organisms. Experiments like these can be important to both guide management decisions and guide future sampling and monitoring efforts when answers are required more quickly than useful theory can be developed.

Despite the benefits of curiosity-driven experiments just described, there are potential problems with relying solely on this type of experiment in ecology (see also Power et al., this volume). The popularity of such experiments arises in part because no thought about conceptual generality is required, and therefore they are relatively easy or less risky to employ. Consequently, these experiments may not provide any general insights by themselves. We have also noticed a recurring misconception about what simple experiments to “see what happens” can do. Specifically, in interacting with colleagues

and speakers at national meetings, we often hear statements such as: "We must conduct an experiment to predict the effect of factor X on the environment." However, experiments do not make predictions; they test predictions (be they as unsophisticated as "factor X has some unspecified effect"). Predictions are only derived from some underlying theory, be it as simple as "if X happens once, I predict that it will happen again." Although this simple prediction might seem reasonable, repeated experiments can often yield surprisingly different outcomes (e.g., Power et al. 1995), suggesting that a more comprehensive and insightful theory would be useful.

Experiments as a Means of Measurement

Often experiments are done to explore the specific functional relationship between the manipulated factor and some response variable of interest. Experimental manipulation often allows the investigator to explore a wider range of variation than is naturally present and therefore obtain a more precise estimate of the functional relationship. In this case, the goal usually is to estimate parameters or identify the shape of their relationship so that reasonable constraints on theory can be applied, rather than to test a specific hypothesis, and consequently this type of experiment does not adhere to the standard formulas of experimental design. Typically, there are a number of different treatment levels used in this approach, and the concept of an unmanipulated control, which is critical for many other types of experiments, is hard to apply or is arbitrary. In ecology, this approach has been underutilized, but as ties between empiricism and theories become more pervasive, we expect these experiments to become increasingly important in ecology.

Perhaps an area where mensurative experiments (defined as experiments where measurements are made on manipulated "treatments" in the absence of a control; sensu Hurlburt 1984) have been most important in determining a functional relationship is in the area of density dependence. There has been a plethora of experiments in ecology designed to detect whether intraspecific competition is an important determinant of organism fitness (e.g., Harper 1977), and the commercial interest in how plant yield is related to initial planting density has been central to this literature. Thus, not only are plant ecologists interested in whether negative density dependence can be demonstrated experimentally in natural populations (Schmitt et al. 1987, Reed 1990), but there is also deep interest in whether the slope of the relationship between plant fitness or yield and planting density is identifiable repeatedly as $-1/2$ on a log scale (Weller 1987, Osawa and Sugita 1989). In addition to the obvious benefits of knowing the strength of negative density dependence in agricultural plots, the strength of negative density dependence critically affects the dynamics of populations (May 1974).

As ecologists have become increasingly interested in the interconnectedness of populations, mensurative experiments that focus on dispersal, gene flow, and migration have increased. For example, Morris (1993) used an experimental array to quantify pollen dispersal by honeybees. The data generated by this array were used to fit diffusion models to pollen dispersal and are ultimately being used to predict how pollen moves as a function of interplant distance, thereby providing insight into how genes from genetically engineered plants might spread. Similarly, Herzig (1995) manipulated

densities of beetle larvae and access to mates to understand the relationship between these factors and rates of beetle emigration. Here the goal was to explore experimentally the factors related to local outbreaks and rapid spread in this leaf-feeding beetle.

Mensurative experiments have also become more important in the investigation of the dynamics of food webs in several ways. First, models with different assumptions about the shape of the functional response (Holling 1959) can yield very different predictions about the consequences of manipulating top consumers and limiting nutrients in food webs (Rosenzweig 1973, Oksanen et al. 1981, Arditi and Ginzberg 1989, Schmitz 1992). Therefore, to guide the development of food web models, experiments that vary prey and predator density are required to examine the shape of functional response surfaces (e.g., Chant and Turnbull 1966, Eveleigh and Chant 1982, Katz 1985). Second, a basic knowledge of the magnitude and distribution of the strength of species interactions is required to place reasonable constraints on food web models. Recent manipulations of various invertebrate grazers on algae (Paine 1992), of various arthropod prey on mantid predators (Fagan and Hurd 1994), and of intertidal avian predators on various invertebrate prey (Wootton 1997) have been conducted to estimate interaction strength. One key result of these studies is that the distributions of interaction strengths appear skewed toward weak interactions (Power et al. 1996), rather than normally distributed as is assumed in many analyses of randomly constructed food webs (e.g., May 1973, Gilpin 1994).

Sometimes experiments that simply introduce variation into a system may be of use in estimating important ecological relationships. A prime example of this approach is the application of PULSE experiments (Bender et al. 1984) to estimate species interaction strength. In PULSE experiments, particular species are perturbed temporarily to move the community from any putative equilibrium, and the short-term rate of change in other species is measured subsequently. We believe that approaches that introduce variation into a system can be extended profitably by taking advantage of the longer term dynamics introduced by either PULSE or PRESS (sensu Bender et al. 1994) experimental manipulations. For example, manipulating bird predators produces a "signal" of known origin that is transmitted to other members of the community, and by applying path analysis techniques the relative strength of interactions among unmanipulated species can be obtained (Wootton 1994a). Such an approach has the potential to be used in conjunction with time-series data of the rates of change of different members of the community through time following the manipulation to provide estimates of the strength of species interactions (Wootton 1994c, Pfister 1995, Laska and Wootton in press).

Experiments as a Means of Testing Ecological Theory

Perhaps the most powerful, or efficient, use of experiments in any scientific discipline is to test theory. Not only do the results of these experiments yield the insights discussed previously for curiosity-driven experiments, but they also usually yield insights into approaches or theories that might (or might not) be applied generally to novel conditions found in other systems or when the particular study system is altered. Experimental tests of theory can address two basic issues: the accuracy of the predictions made by the theory and the adequacy of the assumptions underlying theory.

Testing Predictions When applying experiments to theory, ecologists usually test predictions of the theory. Typically, predictions are more interesting to examine because science is at its best when it predicts previously unestablished results. Testing predictions has been carried out in a variety of contexts. For example, the intermediate disturbance hypothesis (Paine and Vadas 1969, Horn 1975, Connell 1978) predicts maximal species diversity at moderate levels of disturbance. Competitive exclusion through the monopolization of resources is hypothesized to be disrupted by mortality that arises from disturbance, but disturbance cannot be too high or some species may be unable to maintain positive growth rates in the face of such high mortality. Sousa (1979) conducted an experiment designed specifically to test a prediction of this theory by examining the diversity of algal assemblages on intertidal boulder fields. Smaller rocks are less resistant to wave forces, and consequently the organisms living on them experience higher disturbance rates as a result of rolling. By experimentally stabilizing rocks, Sousa effectively reduced disturbance rates, and diversity increased as a result, in accordance with the model. This example can be used to illustrate the power of linking experimental tests to theory. Because of the underlying theory used to motivate the test, Sousa's results potentially have implications for our understanding of the effects of disturbance in a variety of forms on a range of other systems. In the absence of this theoretical link, they would only show that rolling rocks have an effect on diversity in an intertidal boulder field in California.

Experimental tests of theoretical predictions can also be usefully applied to theories that examine interactions among species at multiple trophic levels with variations in productivity (e.g., Rosenzweig 1973, Oksanen et al. 1981, Arditi and Ginzberg 1989). Such models are interesting because they provide an avenue to link ecosystem-level features (variations in productivity) with community-level processes (trophic interactions). Depending on the assumptions about the relationship between predator consumption rates and both prey and predator densities, different predictions are obtained regarding how different trophic levels should change as productivity changes. For example, if per capita consumption rates are functions of prey densities, increasing productivity will only increase certain types of consumers and producers (Rosenzweig 1973, Oksanen et al. 1981), whereas if per capita consumption rates are functions of the ratio of prey to predator densities, all trophic groups should change together (Arditi and Ginzberg 1989, Schmitz 1992). Experimental manipulations are required to test these predictions because observational comparisons across systems are confounded by changes in species composition, which distort the predictions of the models (Mittelbach et al. 1988, Persson et al. 1988, Leibold 1989). Experimental manipulations of productivity in a river, designed specifically to test these predictions, show that producers and predators, but not grazers, increase with increasing productivity (Wootton and Power 1993). Experimentally elevating levels of limiting nutrients or light in ponds, streams, and rocky intertidal shores increases grazers but not algae (Leibold 1991, Leibold and Wilbur 1992, Hill et al. 1995, Wootton et al. 1996b). These results are more in accordance with the predictions of prey-dependent models than those of ratio-dependent models.

Experiments have also been applied extensively to test predictions from life history theory. Experimental manipulations of offspring number (e.g., Vander Werf 1992,

Young 1996) have been done in an effort to test Lack's (1947) hypothesis that clutch size has evolved toward the number which produces the most offspring. Similarly, experimental manipulations of the level of commitment to reproduction (e.g., Snow and Whigham 1989, Pfister 1992) have been a commonly used means of detecting whether there is a cost of reproduction, as proposed by Williams (1966). Experiments have been especially powerful in this context, since erroneous correlations can be estimated when treatments are not randomly assigned among individuals (Reznick 1985, Pease and Bull 1988). Indeed, in a summary of published results, Reznick (1985) found a marked difference in the proportion of studies that found reproductive costs with correlative versus experimental methods. Correlative, nonexperimental results ('phenotypic correlations') demonstrated a cost with a lower frequency (22 of 33) than that of studies that manipulated experimentally the level of reproductive investment (17 of 20).

Experimental tests of theoretical predictions can be especially useful when applied to tractable systems as a proxy for intractable systems. Thus, we advocate increased validation of theory or observational approaches in systems where experiments are easily performed before applying such techniques in experimentally intractable situations. We illustrate this point by considering how observational approaches have been used to gain insight or make predictions about the strengths of species interactions in natural communities. As a first example, one common approach assumes communities are at equilibrium and uses regressions of species abundances in different locations to derive an index of interspecific interactions (Schoener 1974, Hallett and Pimm 1979, Pimm 1985). When applied to an assemblage of tide pool fishes that are amenable to experimentation, this technique predicted mutualistic interactions among species after factoring out habitat variation (Pfister 1995). In contrast, an experimental manipulation designed in part to test this approach demonstrated strong asymmetric competitive effects among species (Pfister 1995), effects predicted using an alternative, nonequilibrium approach that estimates rates of population change over time as a function of initial community composition.

As a second example, another approach toward evaluating community structure imposes an experimental perturbation on the community, allows unmanipulated members of the community to respond, and applies path analysis, a technique designed to disentangle the relative strengths of different direct and indirect pathways among variables (Wootton 1994a). By following the signal of the perturbation through the community, path analysis can predict other potentially strong interactions in the community. Results of experimental manipulations of birds in rocky intertidal communities were analyzed using this technique, which predicted the effects of other types of manipulations involving acorn barnacles, goose barnacles, snails, and birds (Wootton 1994a). Follow-up experimental manipulations tested the predictions of the approach, and the results indicated that the experimental/path analysis approach has some validity (Wootton 1994a).

A third example involves combining observational data on feeding rates, predator behavior, predator density, and prey density to produce a theoretically appropriate measure of per capita interaction strengths among consumers and resources. Experimental manipulations of intertidal birds (gulls, oystercatchers, and crows) that tested relevant predictions for a variety of different prey quantitatively fit the predicted interaction strengths, indicating that certain types of observational measures might be of use in

identifying strongly interacting species in experimentally intractable communities (Wootton 1997).

Testing Assumptions An often ignored but potentially powerful use of experiments to test theory is to evaluate the assumptions rather than the predictions of theory. Perhaps the best illustration of the power of experimentally testing assumptions is work examining Darwin's theory of evolution by natural selection (Darwin 1859). Authors have argued (Waddington 1957; Birch and Ehrlich 1967; Peters 1976, 1991) that Darwin's theory should be discarded because it makes either untestable or circular predictions. Why, then, does this theory still retain its central place in biology? The weakness in the circularity/testability argument is that it supposes that only the predictions of theories are open to testing when, in reality, evaluating the assumptions of theories provides a far more stringent test (see Dayton 1973, Holt 1977). Darwin's theory is actually very testable. It rests on three assumptions: (1) variation exists between individuals in the traits they possess; (2) the variation is (at least to some extent) heritable; and (3) differences in traits produce differences in survival and/or reproduction (i.e., natural selection exists). All of these assumptions have been overwhelmingly supported. Common garden experiments, classical breeding experiments, and experimental molecular genetics have clearly demonstrated that assumptions (1) and (2) are true (Futuyma 1986). Numerous ecological and morphological experiments have generally demonstrated that assumption (3) is true (e.g., Endler 1986). These experimental tests of assumptions, rather than predictions, leave little doubt as to the applicability of Darwin's theory to biological systems.

Testing assumptions has also played an important role in community ecology. For example, a fundamental assumption of many models is that competition plays an important role in structuring communities (e.g., Lotka 1925, MacArthur and Levins 1967, Schoener 1974, Diamond 1975, Roughgarden 1976, Tilman 1982, Chesson 1983). In response to criticism that such an assumption might be unwarranted (Connor and Simberloff 1979, Strong et al. 1979), a number of experiments have been conducted specifically to test this assumption in a variety of communities (e.g., Pfister 1995, reviewed in Connell 1983, Schoener 1983, Goldberg and Barton 1992, Gurevitch et al. 1992). In reading the recent literature, however, our impression has been that the motivation for experimental tests of competition has increasingly drifted away from testing assumptions of ecological theory. Instead, recent experiments have tended to ask only, What happens when a potential competitor is removed from a particular community? Ideally, the results of such experiments should be pursued for their broader implications—for example, probing whether predictions from different competition-based models are upheld and, if they are not, determining the underlying mechanisms (e.g., Creese and Underwood 1982, Schmitt 1996).

A related consideration is that finding negative results in competition experiments does not necessarily mean that competition is unimportant in determining community structure. Most experiments that test for competition examine the simple prediction that reducing one species will increase the population of its competitor. When interspecific competition operates in conjunction with other processes, however, a variety of compensatory effects may hide the negative effects of competition, even when interspecific competition is strong (Fig. 18-1; see Davidson et al. 1984, Fairweather 1990 for ex-

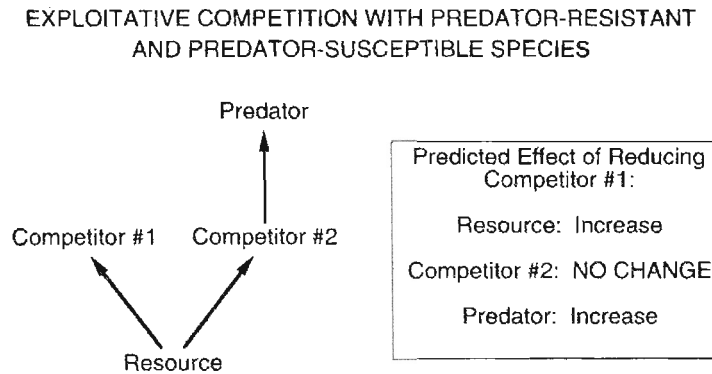


Figure 18-1. An example where competition would play an important role in community structure, but manipulations of one competitor would fail to reveal its negative effects on the other competitor. If competitor #1 was reduced in abundance experimentally, competitor #2, rather than increase, would experience no change in abundance, while the predator would increase. The increase in predator abundance compensates for the increased productivity in competitor #2 that results from competitive release.

amples). Thus, finding a negative result may permit the conclusion that a model based solely on interspecific competition is inadequate, but it may not necessarily refute models with the assumption that competition is one of several important interactions that are occurring (e.g., Leibold 1996).

Another area where tests of assumptions might be profitably applied in community ecology revolves around the issue of how multispecies models can be constructed. The simplest approach is to examine linked dynamical equations describing direct interactions among species (*sensu* Wootton 1994c), such as the community matrix approach used by Levins (1969), May (1973), Levine (1976), Pimm (1982), Yodzis (1988), and others. A fundamental assumption of these models is that the per capita effects of one species on another are unaffected by the abundance of other members of the community (i.e., instantaneous effects of each species can be added together in differential equations without including "higher order" terms that incorporate simultaneously the abundances of more than one interacting species). Early examinations tested predictions of models with this assumption and, when predictions deviated from the results, concluded that the assumption was incorrect (e.g., Wilbur 1972, Neill 1974, Morin et al. 1988, Pfister and Hay 1988, Wilbur and Fauth 1990, Wootton 1992, 1993a). However, a number of alternative factors (nonlinear pairwise interactions, asymmetries in experimental and theoretical time scales, theoretically inappropriate data transformations, and other types of indirect effects) make interpretation of deviations between observed and predicted results very difficult (Case and Bender 1981, Pomerantz 1981, Adler and Morris 1994, Billick and Case 1994, Wootton 1994b). An alternative approach is to focus on the mechanistic interpretation of the assumption (that the effects of one species on another are not modified by the abundance of other members of the community; see Wootton 1993a, 1994b, 1994c) and conduct experiments that directly address this assumption.

This involves preventing other members of the community from changing the abundance of the focal pair of interacting species and observing whether the net effects of the interaction change as a result. For example, Werner (1992) and Wissinger and McGrady (1993) were able to change the interactions between frog tadpoles and odonate nymphs, respectively, by introducing a predatory odonate species that was prevented from feeding. An additional issue raised in work that examines this assumption is whether it is necessarily a good idea to discard a model even if the assumptions are demonstrated to be incorrect. In many cases, the critical question is whether failure of the assumptions severely affects model predictions, since virtually all models have some simplifying, incorrect assumptions. For example, Morin et al. (1988) found patterns in experimental pond communities that indicated that effects of two species on a third target species were not independent but pointed out that the additional explanatory value of accounting for the interactive effects of the two species was slight.

In addition, testing the assumptions of ecological theory may often be possible when testing predictions is intractable, just as in the case of evolution by natural selection. For example, theories that address how species coexist may fall into this category. In the case of the "storage effect" model for coexistence (Warner and Chesson 1985, Chesson 1994), the assumptions are relatively straightforward and testable: (1) the species compete; (2) species experience effective bouts of recruitment at different times; (3) species have relatively high adult survival, and competition and environment variation affect survival relatively little; and (4) species can increase from low density. However, the prediction of the storage effect model is that species coexist locally due to the preceding four criteria being met. To test the prediction of the storage effect model ignores other potential mechanisms of coexistence.

Testing the assumptions of ecological theory may also be more feasible ethically. For example, a number of authors have recently used metapopulation models to explore coexistence among competing species (Tilman 1994, Tilman et al. 1994, Kareiva and Wennergren 1995). In these models, it is assumed that there is a trade-off between competitive ability and colonization success. Superior competitors always replace inferior competitors in "patches" of solitary individuals, and inferior competitors are capable of colonizing empty patches at a greater rate. Another assumption involves the initial distribution of species abundance (e.g., a geometric series of species abundance was used by Tilman et al. 1994). One of the predictions made by these models is that increasing habitat destruction or degradation results in an increased probability of loss of the superior competitor (Tilman et al. 1994). Clearly, in many systems testing the prediction of how habitat loss affects species abundance patterns may be prohibitive if manipulating experimentally the loss of habitat is unethical or impossible. Thus, for systems in which the predictions of the theory have the most conservation importance, testing assumptions of the models may be the only way to evaluate their relevance.

Testing the assumptions of theory may be as or more rigorous than testing the predictions. Darwin had enough natural history insight to derive a theory based on several simple (and ultimately upheld) assumptions. However, many ecological theories do not share these qualities, and often these theories consist of a number of simplifying assumptions. In addition, one problem with testing the assumptions of a theory is that the status of the theory is unclear if we cannot uphold experimentally one or several of the assumptions. Consider the storage effect model again. If we test the assumption

that species compete in a particular system and find out they do not, then this finding would indicate strongly that we should not use the storage effect model. If, however, we find that adult mortality can be relatively high at times, in contradiction to a storage effect model assumption, then do we dispense with the model? The latter scenario does not yield a clear answer. Minimally, experimental tests of assumptions should reveal to us where theory needs modification.

We believe that experimental tests of the underlying assumptions of ecological theory are underutilized and offer one instance where they could be utilized more. The theory that subpopulations might be distributed as metapopulations has yielded a variety of metapopulation models that describe the occupancy of discrete habitat through time with differential equations (Levins 1969, Hanski 1982, Gotelli 1991). Although a variety of assumptions underlie all models, the assumptions that distinguish among models are how they relate extinction and colonization rates to habitat occupancy. Although several investigators have used census data to explore how extinction and colonization rates relate to occupancy (Gotelli and Kelley 1993, Hanski et al. 1995, Pfister in press), we are aware of no studies that have manipulated experimentally either extinction, colonization, or occupancy to determine the relationship. As the use of previously formulated metapopulation models grows (Gotelli and Kelley 1993, Tilman 1994, Hanski et al. 1995, Pfister in press) and the derivation of new metapopulation models increases (Hanski and Gyllenberg 1993), empirical tests of metapopulation model assumptions are sorely needed.

The Context of Experiments

The Interplay of Questions and Experimental Approaches

Aside from differences in experimental approaches that arise from the three general approaches outlined previously, differences may also arise because of different specific questions of interest, even when studying the same general phenomenon. One example is in the study of interspecific competition. Ideally, experimental treatments that test for the effects of competition should be designed such that each target species of interest is examined at a control density (preferably that found in the natural environment), at a control density in combination with a putative competitor species (again, preferably at its natural density), and as a single species at a density equal to the total density in the mixed species treatment. This design permits detection of interspecific competitive intensity, intraspecific competitive intensity, and the relative strength of inter- to intraspecific competition (Connell 1983, Underwood 1986; see, e.g., Creese and Underwood 1982, Fauth et al. 1990). In some circumstances, however, the experimental logistics are such that not all treatments can be employed while attaining replication for adequate statistical power. Under these circumstances, the experimental design depends critically on the investigator's interests. If the investigator is initially interested in whether interspecific competition occurs, then treatments should use the control and mixed species treatments (an additive design). If the investigator is more concerned with the relative intensity of interspecific competition to intraspecific competition, which has implications for species coexistence, then treatments should include the mixed species and high-density treatments (a substitutive design). Either design can be appropriate,

depending on the underlying motivation of the investigator, but care should be taken not to overextend the results (for example, concluding that competitive exclusion might result on the basis of the additive design alone). With logistic constraints, the sequential implementation of the two designs might be appropriate, since it is usually not particularly interesting to examine the relative strength of intraspecific and interspecific competition unless interspecific competition is demonstrated. For example, Werner and Hall (1976) conducted an additive experiment which indicated that interspecific competition among sunfish (*Lepomis* spp.) occurs, whereas Werner and Hall (1977) report a substitutive experiment where the relative impact of inter- to intraspecific competition was similar on green sunfish (*Lepomis gibbosus*) but was much higher on bluegill sunfish (*Lepomis macrochirus*).

Similarly, different types of experimental approaches are best suited to alternative strategies that attempt to gain general insights about ecological communities. One possible strategy to address this problem seeks generality through repetitive experimentation across communities and asks what percentage of community variation can be explained by a particular factor (Weldon and Slauson 1986, Underwood and Petraitis 1993). This approach dictates the use of multifactorial experimental manipulations of as many variables as possible, conducted across a number of communities. Complex analyses of variance (ANOVAs) are then applied to estimate the fraction of variation explained by any manipulated factor, which provides an index of the "average" importance of that factor, and to estimate the fraction of variation accounted for by the site by variable interaction terms, which provide indices of how variable the importance of the manipulated factor may be.

An alternative strategy might be to investigate intensively a particular community, develop a detailed mechanistic understanding of its workings, and then explore theoretical and methodological approaches that might generally be applied to other communities. Therefore, in this strategy generality is sought through the development of a flexible theoretical framework that synthesizes a variety of general ecological processes. Obviously, this strategy requires intensive investigation of a target community rather than cross-community experimental comparisons of portions of the community.

Either strategy is valid, given an investigator's interests and philosophy. We personally have opted for the second strategy, for a variety of reasons but particularly because it offers opportunities for generalization to a wider range of communities. First, potential generalization is not limited by the type of organisms present. Thus, the importance of limpets might be determined for a range of rocky intertidal communities, but the result is irrelevant to grasslands, whereas a general theoretical framework for grazing developed by studying limpets might be applicable to bison in grasslands, too. Because generalization in the second approach requires development of process-based theory, it offers the possibility of prediction in novel situations that the first approach does not. On the other hand, it might be countered that the first approach is desirable because its generalizations are unconstrained by particular theoretical constructs. Such constructs are present implicitly, however, as the basis of statistical comparisons (e.g., ANOVA) used to make the generalizations, and the conclusions drawn may be affected by these underlying theoretical assumptions (e.g., Adler and Morris 1994, Billick and Case 1994, Wootton 1994b).

The Place of Experiments in Ecology

Finally, it is worth considering where experiments fit into the general realm of ecological endeavor. In some ways, one's perspective is shaped by the differing approaches to generality outlined previously. The value of current ecological work (as assessed by the content of leading ecological journals) seems to be determined primarily on the basis of whether or not it is experimental (see Power et al., this volume). In some ways, this reflects the philosophy of determining generality through the partitioning of natural variance as outlined previously, although the heterogeneity of experimental design makes it difficult to compare results across systems (Underwood and Petraitis 1993). Meta-analysis of independent experiments may be one potentially useful strategy in addressing this problem (Gurevitch et al. 1992, Wooster 1994, Arnqvist and Wooster 1995). We find, however, that some of the most compelling work in ecology takes a more pluralistic approach that combines experiments, observational information, and theory (see Leibold and Tessier, this volume, for more detailed discussion of the approach). This orientation is more in keeping with the second strategy to obtain generality outlined previously and is often necessary because of logistical constraints on experimentation. For example, Werner and colleagues have developed theory that ties behavioral ecology to species interactions, evaluated its assumptions in small-scale laboratory experiments and medium-scale experimental pond experiments, and tied these results to patterns of variation in the community structure of small lakes and ponds (e.g., Werner and Hall 1974, 1976, 1977; Werner 1984, 1992; Werner and Gilliam 1984; Mittelbach et al. 1988; McPeck 1990; Mittelbach and Osenberg 1993; and references therein). Similarly, the work of Carpenter, Kitchell, and their colleagues unites bioenergetic food web theory, small-scale experiments that calibrate the models and verify their assumptions, whole-lake experiments to test model predictions, and cross-lake comparisons to glean general patterns (see review, in Carpenter and Kitchell 1993). In each of these examples, combining methodologies that individually have different shortcomings (unverified underlying processes, somewhat unnatural small-scale experimental conditions, and lack of replication in experiments under more natural conditions) produces a much deeper understanding of the system.

We have found such an approach profitable in our own work. For example, experiments can rigorously evaluate important local interactions (for example, competition among tidepool fishes or effects of consumers on intertidal succession), but their larger scale implications cannot be assessed without the integration of theory (storage effect [Chesson 1983, 1984, 1994; Warner and Chesson 1985] or local regional models of species interactions [Horn 1975]). Critical, theoretically relevant observational data are also needed, such as patterns of recruitment variation in relation to local or regional abundances, because it is impossible to manipulate large-scale dispersal processes or regional sources of reproduction that affect the local recruitment of marine larvae (Pfister 1993, 1996; Wootton 1993b). Similarly, linking dynamic models of food webs with small-scale laboratory experiments to verify assumptions, mesocosm experiments to evaluate critical processes and predictions, and cross-river comparisons to evaluate the generality of the predicted patterns has proven powerful in investigating the interplay of disturbance, productivity, and species interactions in rivers in the western United States (Wootton and Power 1993, Power et al. 1995, Wootton, et al. 1996a). In sum-

mary, then, we believe that experiments are critical to furthering our ecological knowledge. However, focusing only on experimentation is far less effective than integrating experiment, theory, and observation in a synthetic framework.

ACKNOWLEDGMENTS We are grateful for the perspectives on experimentation we have encountered from numerous colleagues over the years. Among those who have been particularly influential to our thinking are C. Adler, M. Hay, P. Kareiva, L. Johnson, M. Leibold, M. Power, W. Sousa, R. Steneck, and particularly R. Paine. We thank B. Resetarits and J. Bernardo for the invitation to add our thoughts on experimentation to this volume. J. Bernardo, D. Branstretor, J. Chase, L. Cochran-Stafira, M. Leibold, R. Paine, B. Resetarits, and J. Tsao provided helpful comments on the manuscript. This work was supported in part by grants from the Mellon Foundation and the National Science Foundation (DEB93-17980).

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