12
The Need for Large-Scale Experiments to Assess and Predict the Response of Ecosystems to Perturbation

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Summary

Ecosystem experiments are field experiments in which the experimental unit is large enough to include the relevant physical, chemical, and biotic context of the processes being studied. Whole-ecosystem experiments have yielded insights about many processes in a diversity of habitats. Successful design and interpretation of ecosystem experiments depend on connections to theoretical, long-term, and comparative studies. Ecologists have overcome many problems of inference for ecosystem experiments. However, the issue of replication is far less important than the need to compare alternative explanations for the results, which may involve reference ecosystems, premanipulation data, and additional measurements or experiments designed to compare possible explanations. Potential limitations of ecosystem experimentation include the variability and slow dynamics of ecosystems, certain aspects of academic and management culture, and institutional shortcomings. Progress in ecosystem experiments can be accelerated through dedicated sites and funding, and keystones that foster collaborations between management and science for adaptive ecosystem management.

Introduction

Scientific learning takes place through cycles of inspiration, trial, and evaluation. In ecosystem ecology, the trials can take place in the computer and the mind of a theorist, through observations of natural fluctuation in long-term studies, or through comparisons of contrasting ecosystems. Deliberate experimental manipulation of whole ecosystems is a particularly powerful aid to learning. The experimenter causes something interesting to happen, and therefore does not have to wait for an informative event. Moreover, the experimenter knows what was manipulated; this knowledge greatly simplifies the interpretation of events. It is not surprising that ecosystem experimentation has been an insightful and influential component of ecology. It is surprising, however, that ecosystem experimentation is not used more widely to advance the discipline and improve management policies.

Ecosystem experiments are field experiments in which the experimental unit is (1) defined by a useful natural boundary (such as a shoreline or hydrologic divide); (2) large enough to include the relevant physical, chemical, and biotic context of the processes being studied; and (3) deliberately manipulated. Ecosystem experimenters assign high importance to matching the scale of the study to natural or management processes.

This chapter explains the place of ecosystem experimentation in comparison with the other dominant modes of learning about ecosystems, which include theory, long-term observation, and comparison. The diverse accomplishments of ecosystem experiments are also briefly reviewed, and subsequently, the limitations to ecosystem experimentation are discussed: barriers that have been overcome, and barriers that remain. Finally, some steps that could be taken to accelerate progress in ecosystem experimentation are suggested.

Learning About Ecosystems Requires Multiple Approaches

Ecosystem ecology is a table borne by four strong legs, each essential for the intellectual support of the whole (Figure 12.1). The legs are the four major approaches that scientists use to learn about ecosystems: theory, long-term study, comparisons, and ecosystem experiments. Each approach is applied to many types of ecosystems, involves diverse and multidisciplinary practitioners, and creates "invisible colleges" of scientists who read and cite each other's work. Each approach garners substantial intellectual support from the scientific community, and significant financial support from funders of science. Each approach has also been the subject of several influential books in the past decade, and is well represented in this book. Although individual publications of ecosystem ecology have diverse goals, these studies are often motivated by, and find their greatest intellectual significance in, one or more of the four fundamental legs of the science.

The four approaches to ecosystem science have complementary strengths and weaknesses. Because of this complementarity, most ecosystem researchers employ two or more approaches in their own work (Table 12.1). Each approach tends to be applied at certain spatial and temporal scales, and the results tend to be used for certain kinds of inference (Figure 12.2). The four approaches are related to two distinct philosophical perspectives in ecology (Pickett et al. 1994; Holling 1995). One perspective

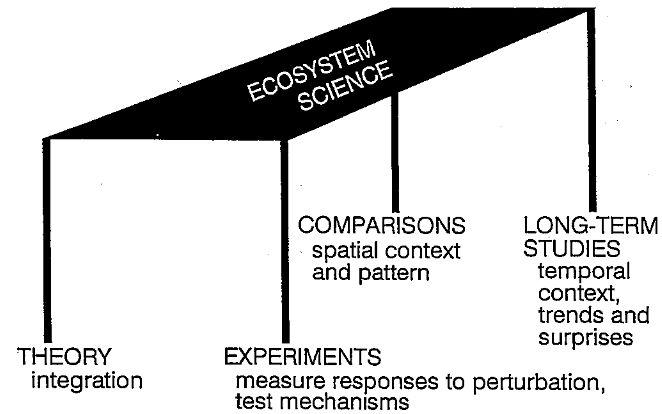

FIGURE 12.1. Ecosystem ecology is similar to a table with four legs essential to the integrity of the whole: theory, comparison, long-term study, and experiment.

is integrative, synthetic, and creative of new explanations and is marked by fertile development of multiple-alternative hypotheses, and comparisons of the degree of corroboration of alternatives. Integration and description represent this philosophy in Figure 12.2. The second philosophical perspective is deductive, experimental, and focused narrowly on the elimination of potential explanations. Deduction and hypothesis testing represent this

TABLE 12.1. Selected strengths and limitations of the four approaches to learning about ecosystems.[1]

Approach	Some strengths	Some limitations
Theory	Flexibility of scale Integration Deduction of testable ideas	Cannot develop without continuous linkage to observation, experiment
Long-term observation	Temporal context Detection of trends and surprises Test hypotheses about temporal variation	Potentially site-specific Difficult to determine cause
Comparison	Spatial or inter-ecosystem context Detection of spatial pattern Test hypotheses about spatial variation	Difficult to predict temporal change or response to perturbation
Ecosystem experiment	Measure ecosystem response to perturbation Test hypotheses about controls and management of ecosystem processes	Potentially site-specific Potentially difficult to rule out some explanations Institutional structures limit scope

1. The limitations arise when one approach is used alone. Usually they can be overcome by combining two or more approaches.

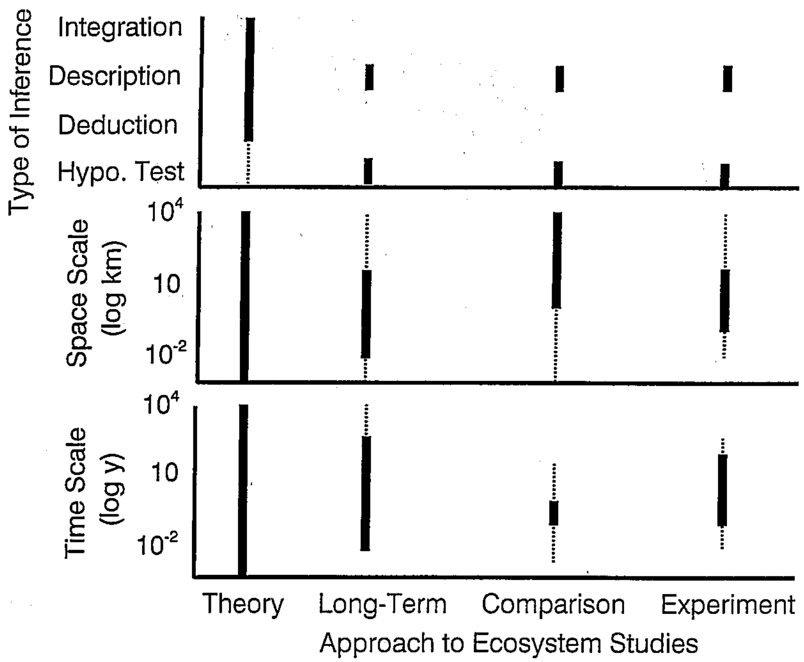

FIGURE 12.2. Comparison of approaches to ecosystem science with respect to type of inference (Pickett et al. 1994), spatial scale, and temporal scale. Solid bars denote primary applications of an approach; dashed lines denote potential or more limited applications of an approach.

philosophy in Figure 12.2. Although both perspectives are essential for progress, ecology has been dominated by deduction and hypothesis testing in recent years.

Theory is essential for integration and deduction, and can be extremely flexible with respect to spatial and temporal scales (Figure 12.2). However, theory must be coupled with observational or experimental research to develop (Table 12.1). Long-term studies have been extremely successful in describing system dynamics and establishing the temporal context for other types of ecosystem studies (Likens 1989). The principal limitation of long-term studies is that the causes of temporal variability may not be apparent. In some cases, mechanisms can be inferred through other approaches, including ecosystem experimentation. Comparative studies have a long and successful record of describing broad patterns in ecosystems and establishing the spatial context for ecosystem studies (Cole et al. 1991). The principal limitation of comparative studies is that they are often based on regressions fit to data from many ecosystems and may be unable to predict how a given ecosystem will respond to a change. In some cases, the capacity for site-specific predictions can be improved by using theory, ecosystem experiments, or local long-term studies. Ecosystem experiments have successfully

measured effects of manipulations and tested hypotheses at relatively large spatial scales, including scales relevant to environmental management (Likens 1985; Mooney et al. 1991; Carpenter et al. 1995). The principal limitations and challenges of ecosystem experiments are elaborated in the next sections. Design of successful ecosystem experiments requires theory (to provide intellectual context and suggest those questions that are worthy of experimentation) and the spatial and temporal context provided by comparative and long-term studies.

Large-Scale Experiments Have a Unique and Essential Role in Ecology

Experimentation at the spatial and temporal scales of natural ecosystem processes has unique and important advantages. This type of experiment is the only research approach that tests responses to known perturbations directly at the ecosystem scale. Ecosystem experiments can match the scale of management, and can provide results directly applicable to environmental policy and management.

Ecological systems do not have a single characteristic scale, and ecological concepts, measurements, and experiments are usually scale-dependent (Levin 1992). Insightful ecological experiments have been performed at a wide range of scales, and it is often valuable to nest experiments at several different scales (Frost et al. 1988). This chapter does not promote any particular scale as being optimum for ecological experiments; however, it does argue that relatively large-scale experiments provide vital information that cannot be obtained by other approaches. Ecosystem experiments are the only approach that measure effects of changing key variables in the context of other major controls of ecosystem processes. Comparative and long-term studies assess context without direct manipulation, and small-scale experiments study mechanisms out of context.

Small-scale experiments cannot substitute for ecosystem experiments because crucial ecosystem processes are distorted or excluded by the small size and short duration of microcosm experiments. Microcosm experiments cannot include such wide-ranging or slow processes as large-scale turbulence, wide-ranging predators, or large, slow-growing trees. Some small-scale processes quickly reach unrealistic rates in microcosms ("bottle effects"); these include microbial production and biomass, and phytoplankton production. Some examples of misleading results from experiments that were too brief or too small are given by Tilman (1989) and Carpenter (1996). These points, however, do not negate the value of small-scale experiments for testing and measuring mechanisms. They only emphasize the difficulty of extrapolating measurements from small-scale experiments to larger scales in which the key controls of ecosystem processes may be different.

The fundamental problem with learning from small-scale experiments is that results must be translated across scales to draw conclusions about ecosystems. Projection across scales is a very difficult process, and the models are complicated, context-specific, and subject to considerable debate and research (Allen and Hoekstra 1992; Levin 1992). Conversely, inference from ecosystem experiments requires fewer assumptions because appropriate scaling can be taken into account by the experimental design. Thus, ecosystem experiments are convincing tests of basic ecological ideas. The scale of ecosystem experimentation is especially useful in environmental management because it is very difficult to convince managers or other stakeholders to change policies using complex arguments and extrapolations (Lee 1993). Direct results from appropriately scaled experiments are simpler, obviously relevant, and, therefore, more apt to influence policy.

Large-Scale Experiments Have Succeeded in Diverse Circumstances

Insightful ecosystem experiments have succeeded in diverse circumstances (Table 12.2). Indeed, many different types of ecosystems have been manipulated. Independent variates have included physical, chemical, and biotic factors, and in some cases, tracers have been added to large systems to measure process rates (e.g. Bower et al. 1987; Coale et al. 1996). Dependent variates have included such ecosystem processes as production or nutrient cycling, as well as community and population processes. Additionally, large-scale experiments have considerable value in community ecology as well as ecosystem ecology (Lodge et al. 1997).

Inadvertent disturbances, caused by either natural or human events, have also yielded valuable insights. Inadvertent disturbances are especially useful when predisturbance data exist, and when undisturbed reference areas have been studied (i.e. when they resemble deliberate manipulative experiments). Consequently, the most useful information from inadvertent disturbances probably occur at sites of ongoing, long-term studies. For the purposes of this chapter, inadvertent disturbances are classified as a component of long-term studies, and the focus is instead on deliberate manipulations.

Measuring the magnitude of response to manipulation and understanding our capacity to manage are the two most common reasons for ecosystem experimentation. Some ecosystem experiments, however, are performed purely to test ecological ideas. One example of this type of experiment is the research on trophic cascades, which was designed primarily to test ideas about the effects of aquatic community structure on ecosystem processes (Carpenter and Kitchell 1993). Other experiments are primarily environmental demonstrations. For example, the Risdalsheia acidification experiments showed, in a clear and dramatic way, that watersheds could recover rapidly if the acid was removed from precipitation (Wright et al. 1988). Some experiments are conducted in a management context, in which the primary goal is to improve management of a resource and learn in the process. Fisheries experiments, for example, have been used to explore effects of contrasting harvest policies on fish production (McAllister and Peterman 1992; Walters 1993). In fact, many ecosystem experiments have multiple goals. A good example of a multiple-goal experiment is the Hubbard Brook deforestation studies (Likens et al. 1978). Initial studies were motivated by very basic questions, but later experiments were

TABLE 12.2. Selected examples of ecosystem experiments.[1]

Ecosystem Type	Independent Variates	Dependent Variates	Reference
Lakes	Lime addition	Fish production	Hasler et al. 1951
Lakes	Nutrient addition	Primary production	Schindler 1977
Lakes	Acid addition	Biogeochemical cycles, food webs	Schindler et al. 1991
Lakes	Fish-community manipulations	Primary production, nutrient cycles, food webs	Carpenter and Kitchell 1993; Gulati et al. 1990
Open ocean	Iron addition	Primary production	Coale et al. 1996
Great Barrier Reef	Fishing	Fish production, community composition	Walters 1993
Streams	Insect removal	Carbon export	Wallace et al. 1996
Streams	Acid addition	Chemical and biological exports	Hall and Likens 1981
Catchment and stream (boreal forest)	Acid addition, exclusion	Chemical exports	Wright et al. 1988
Boreal forest	Acid addition, liming	Soil chemistry, biology, forest production	Abrahamson et al. 1994
Boreal forest	Nutrients, forage, predator exclusion	Snowshoe hare population	Krebs et al. 1978
Deciduous forest	Forest harvest, herbicides	Hydrology, nutrient export	Likens et al. 1978
Tallgrass prairie	Fire frequency	Nitrogen and carbon cycle, species composition	Ojima et al. 1994; Gibson et al. 1993

1. This table is intended to illustrate the diversity of ecosystem experiments, and is far short of a comprehensive list.

intended to compare forest-harvest practices to determine how forests could be harvested in a sustainable way.

Some Significant Barriers Have Been Overcome

Ecologists have identified and overcome some important barriers to ecosystem experimentation. Practical barriers include access to sites, sustained financial support, and the capacity to manipulate and study large systems. The examples reviewed here (Table 12.2) and many others show that sometimes these barriers have been overcome, often by ingenious means but occasionally by persistence and good luck. Nevertheless, access to sites, sustained financial support, and mechanisms for collaboration of scientists and managers often pose barriers to ecosystem experimentation.

Ecosystem experimenters often must choose between the need to apply strong, sustained manipulations that cause a clear, interpretable response and the need to understand effects of more modest or gradual perturbations. For example, an experiment may double the atmospheric carbon dioxide concentration immediately, but the global impacts of doubled carbon dioxide concentrations will actually develop gradually over decades. In this particular case, models and long-term trend studies provide additional information that is crucial for interpreting and applying the experimental results to predict ecosystem change. Studies of the effects of nutrients and food-web structure on lake productivity demonstrate a combination of experiments with comparisons and theory (see Smith, chapter 2). Comparisons show that whole-lake manipulations of nutrients and food webs are substantial, yet within the ranges known for many lakes (Carpenter et al. 1991). In general, extensions of experimental results will require some integration with theory, and long-term and comparative studies (Figure 12.1).

Inference poses significant intellectual challenges that have been met in many ecosystem experiments. Inference is the process of deciding upon an explanation for the experimental results. When a scientist argues for a particular explanation, there is an obligation to show that the favored explanation is more probable than all plausible alternatives. This process involves results of the experiment itself and external information (e.g. observations and theory from other studies). Hilborn and Mangel (1997) discuss the process of inference using multiple alternative hypotheses.

Reference ecosystems are unmanipulated ecosystems that are expected to experience the same regional trends (e.g. climate) as the manipulated ecosystems. A.D. Hasler introduced the term "reference ecosystem" (instead of "control") to acknowledge the fact that no two ecosystems are identical, therefore pretreatment conditions in experimental and reference ecosystems cannot be controlled as thoroughly as in a laboratory experiment (Likens 1985). Reference ecosystems are used to check the possibility that responses of the manipulated ecosystem were caused by regional trends and not by the manipulation; they are also used to measure the variability of an undisturbed ecosystem, to help determine whether the response of the manipulated ecosystem can be explained by random variations (Carpenter 1993). Since the pioneering work of Hasler et al. (1951), most ecosystem experimental designs have included reference ecosystems.

The possibility that random variations can explain any apparent responses to the manipulation can be checked using statistical methods. All such methods depend on having multiple observations of the experimental ecosystem both before and after the manipulation. "Before and after" data (i.e. premanipulation and postmanipulation) are necessary even if there is a reference ecosystem (Stewart-Oaten et al. 1986) because ecosystems are never identical, and it is necessary to have a measure of the differences between reference and experimental ecosystems prior to manipulation. In general, premanipulation and postmanipulation data are compared using a statistic that accounts for the variability in the data, which is measured using repeated observations through time. The analysis can include information from both reference and manipulated ecosystems (Stewart-Oaten et al. 1986; Carpenter et al. 1989). Serial dependency in the time series of observations can strongly affect the results but time-series methods can correct for any biases caused by serial dependency (Carpenter 1993; Rasmussen et al. 1993). The most commonly used time-series methods assume that observations are evenly spaced and that there are no missing data. Bayesian time-series methods relax these assumptions and appear to have great promise for analysis of ecosystem experiments (Pole et al. 1994; Cottingham and Carpenter 1998).

The issue of pseudoreplication (Hurlbert 1984) has created considerable confusion in ecosystem ecology. The definition of a replicate is a matter of scale and if the research question applies to a singular ecosystem, then no genuine replicate is possible. Sampling should measure the relevant spatial and temporal variability of the ecosystem before and after manipulation, and methods cited previously can be used to check the possibility that the responses are merely random (Stewart-Oaten et al. 1986). If the research question applies to a larger universe (e.g. "all dimictic lakes"), then replicates could be drawn randomly (i.e. from the world's dimictic lakes), assigned randomly to treatments, and compared statistically (Hurlbert 1984). In practice, of course, this is impossible. Ecosystem experiments are usually unreplicated, and may be viewed as case studies or system-specific investigations. In a few situations, however, particularly interesting ecosystem experiments have been repeated in many parts of the world. Comparative analyses of such sets of experiments can be valuable (e.g. Schindler et al. 1991) and statistical methods do exist for pooling data to evaluate hypotheses across multiple experiments (Gurevitch and Hedges 1993; Gelman et al. 1995).

Measuring the magnitude of ecosystem response is generally far more important than testing the null hypothesis. Manipulations are designed to produce the effect so that it can be studied (Carpenter 1989); the null hypothesis is obviously false. By the time we are convinced to invest in an ecosystem experiment, there is usually considerable evidence that the manipulation will have some effect. The important questions have to do with the nature and magnitude of the effect. The appropriate statistics are often descriptive, for example, means or confidence intervals (Hurlbert 1984) and Bayesian analyses provide far more useful information than conventional statistics (Box 12.1).

Nevertheless, replication can substantially increase the value of ecosystem experiments. In the most obvious case, a replicate is appropriate if

Box 12.1

Ecosystem experiments are often used to measure the response to a specified manipulation. Because ecosystem responses are inherently variable, it is natural to describe them using probability distributions. Bayesian analysis is the branch of statistics used to calculate probability distributions for experimental responses (Gelman et al. 1995).

An example of a probability distribution for an ecosystem response is depicted in Figure 12.3. In this experiment, dense beds of an invading aquatic plant (Eurasian water milfoil, *Myriophyllum spicatum* L.) were harvested in channels designed to increase habitat for fishes (bluegill, *Lepomis macrochirus* L.) (Carpenter et al. 1997). Annual bluegill growth was measured in four experimental lakes and six reference lakes before and after manipulation. The probability distribution for the improvement in growth in the manipulated lakes relative to the reference lakes was calculated (Gelman et al. 1995).

The distribution presents a substantial amount of useful ecological information. Most of the area of the distribution lies above zero (about 98%), indicating a 98% probability that bluegill growth increased and only a 2% probability that bluegill growth decreased. The peak of the distribution, indicating the most probable magnitude of the increase, lies at about 10 mm. The probability of a growth increase of 10 mm is about 0.11, while the probability of a growth increase of 0 is about 0.01, therefore we are eleven times more apt to see a growth increase of 10 mm than we are to see no growth increase. On the other hand, a growth increase as large as 20 mm is much less probable than a growth increase of about 10 mm. An additional 10 mm of growth is a substantial increase for bluegill, which typically grow about 25 mm in their third growing season (Carpenter et al. 1995).

In contrast, the information from a typical statistical test (in this case, a simple student t-test comparing manipulated and reference

Box 12.1 *Continued*

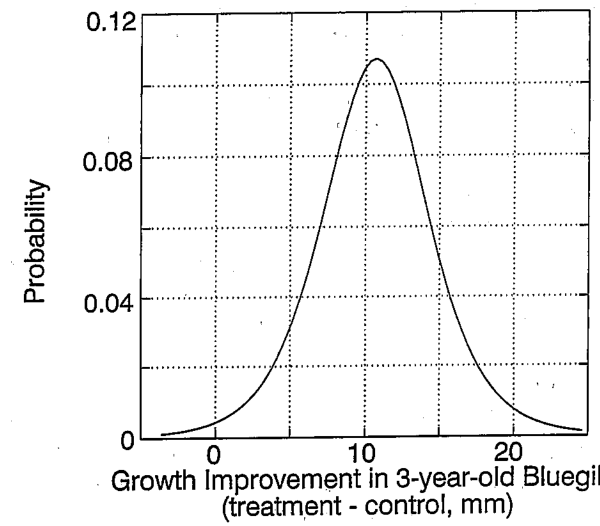

FIGURE 12.3. Probability vs. growth improvement in three-year-old bluegill caused by removal of Eurasian water milfoil.

ecosystems) contains little useful ecological information. Unlike the Bayesian analysis, the conventional analysis does not determine the probability that we most want to know (i.e. the probability that the manipulation caused the effect). Rather, all probabilities are risks of error associated with particular decisions toward the null hypothesis that the manipulation had no effect. If we reject the null hypothesis of no growth improvement in manipulated lakes, the probability of making an error is 0.0243. If we accept the null hypothesis, the probability of making an error depends on the actual size of the improvement in bluegill growth. If the actual growth improvement is 10 mm, then the probability of error if we accept the null hypothesis is about 0.9 (Carpenter et al. 1995). The t-test calculations reveal that the most probable growth improvement is 10.4 mm, but provide no estimate of the odds of this growth improvement relative to other such values as 0 mm or 20 mm. The information provided by the conventional statistical analysis is considerably more complex than the information provided by the Bayesian analysis, and is far less relevant to the ecological question that motivated the experiment.

For introductions to Bayesian inference in ecology, see Ellison (1996) and Hilborn and Mangel (1997). Gelman et al. (1995) present methods and computational approaches; Howson and Urbach (1989) discuss the use of Bayesian evidence in scientific reasoning.

there is a good chance that the manipulation will have no effect (McAllister and Peterman 1992; Carpenter et al. 1995). The conclusion that the manipulation has no effect is far more credible if it is based on data from several different ecosystems.

The great value of replicate ecosystems is not statistical power, but rather the opportunity to evaluate additional possible explanations for the results. Replicates allow the investigator to explore the possibility that these particular results apply only to a single ecosystem, and thereby assess the generality of the conclusions. Replicates also allow the investigator to assess the effects of other factors that may have caused the results. For example, were the results brought about by unusual environmental conditions in the particular time period that the manipulation was performed (Walters et al. 1988)? This possibility could be checked by performing the same manipulation on a similar ecosystem in a different year.

Generation and comparison of alternative hypotheses are the cornerstone of scientific creativity (Pickett et al. 1994; Holling 1995). An effective ecosystem experiment anticipates the alternative hypotheses and includes methods for evaluating and comparing them. There are excellent statistical methods for comparing the credibility of alternative hypotheses (Jefferys and Berger 1992; Hilborn and Mangel 1997), but unfortunately these methods are underused by ecologists. However, the key arguments depend not on statistics, but on effect sizes (and their variability), careful checking of alternative possibilities, and ecological reasoning.

Some Significant Barriers Remain

Ecologists have clearly demonstrated that insightful experiments can be performed on large, complex systems. There are, however, a number of limitations or barriers to ecosystem experimentation.

Some barriers cannot or should not be overcome and not every ecology question requires an ecosystem experiment. Ecosystem experiments will always be relatively costly, and we need to choose carefully those experiments that have priority. There are also ethical and environmental limitations; perhaps there are some ecosystem experiments that simply should not be done.

Substantial barriers may exist even for experiments that have high priority for science and society. The next section considers limitations created by the dynamics of ecosystems, academic culture, the culture of management, or the institutions that conduct ecosystem experiments.

Limitations Posed by Ecosystems

Variability, slow dynamics, and multiple-interacting controls of ecosystems pose significant challenges to experimentation. Because of these properties, some questions cannot be answered by ecosystem experimentation and must be addressed by other approaches. There are perhaps questions that are not susceptible to any approach presently available, but that issue is beyond the scope of this chapter.

Ecosystems can be highly variable in time and space. Long-term and spatially intensive studies are an effective (but potentially costly) way of coping with variability. Alternatively, ecologists can choose to focus on variates that have tractable variability. In lake phytoplankton, for example, ecosystem variates (total biomass or production) and allometric variates (aspects of community-size structure) are far less variable and more predictable than population sizes or the taxonomic composition of communities (Cottingham and Carpenter 1998). Consequently, clear inferences are possible in lake ecosystem experiments focused on biomass, production, and size structure of plankton. The responses of populations of species are more variable and hard to interpret, however. In terrestrial ecosystems, there may be comparable patterns that would suggest those variates that are most appropriate for experimentation.

Ecosystem dynamics can be very slow, and therefore it is difficult to study them for a long enough period of time to perceive the response. Ecologists have coped with this problem through experimental designs that accelerate change (Carpenter and Kitchell 1993), comparative studies that substitute spatial patterns for temporal ones (Pickett 1989), and direct long-term observation (Likens 1989). When ecological dynamics take longer than the careers of investigators, it is essential to create institutions capable of sustaining the research. The U.S. Long-Term Ecological Research (LTER) network is an effort to create such institutions.

Controls of ecosystem processes also change over time (Levin 1992; Holling 1995). Transitions in key controlling processes pose special problems for long-term experiments, because it is very difficult to account for them in the experimental design. Walters (1986) has studied this problem for fisheries where the goal is to manipulate fishing intensity to measure effects on fish production rate. But fish production rate can also be controlled by other "hidden variables," which are not set by the experimenter and may not even be measured (e.g. climate, forage fish production, and so forth). If the experiment can be conducted in a time span that is long enough to account for several natural fluctuations in the hidden variables, or short enough that the hidden variables do not change, then the experiment is apt to succeed. But if the time span of the experiment is near the cycle of fluctuation in the hidden variables, the experiment could be confounded. A good description of the system through long-term studies, or repeated manipulations over several cycles of the hidden variables, may help to resolve this problem.

Barriers from Academic Culture

Academic culture poses several barriers that need to be considered and overcome by ecosystem experimenters. Academic reward systems often favor research that is sharply focused and of a narrow discipline, instead of broadly relevant and interdisciplinary. In ecological terms, intense competition for limited research resources drives academics into narrower and more rigorously defended niches. This type of environment favors research on systems that are well controlled, carefully defined, and simple. It is not an environment that selects experiments about complex, variable, and unpredictable ecosystems, which require long-term studies and cross-disciplinary collaborations in areas in which knowledge is incomplete and evolving.

Academic standards for hiring, promotion, and tenure create pressure for fast publication (relative to slow ecosystem responses) and aversion to interdisciplinary multiauthored publications. In some departments, applied research is viewed as less valuable than basic research. There has been progress in breaking down these barriers, but young scientists are sometimes averse to multiauthored publication. The community of ecologists can accelerate progress by recognizing and rewarding research that is appropriately scaled, collaborative, cross-disciplinary, and useful.

Ecosystem experimentation can also be an excellent context for graduate training. Even though the experiment itself may take too much time for a thesis project, insightful student projects can often be designed around pretreatment studies, modeling, retrospective analyses or other aspects of the experimental program. The multidisciplinary nature of ecosystem experiments and interactions with management agencies can create extraordinary opportunities for graduate students. Graduate programs, however, may not be well-positioned to obtain the maximum benefit from these opportunities.

Traditionally, graduate training has been viewed as a simple student–mentor process, and academic rewards and resources have been allocated accordingly. However, in modern interdisciplinary research it "takes a whole village to train a graduate student." We need to improve our mechanisms for training students in team research. Academic mechanisms and funding should be developed for multi-mentored, cross-disciplinary doctoral projects and students should be rewarded and recognized for their contributions to teams.

Barriers from the Culture of Management

The culture of management also poses significant barriers to ecosystem experimentation. Gunderson et al. (1995) observed that management systems follow an adaptive cycle through time. Peaks of adaptability and receptivity to learning are followed by troughs of bureaucratic stasis when learning is impossible. During periods when policies appear to be working, management systems become more streamlined and narrow. Monitoring and research programs may be abandoned in order to focus resources more efficiently on policy objectives. Even as the management system is becoming more rigid, the ecosystem and society's expectations are changing in ways that can make the policies myopic and irrelevant. Eventually it can become clear that the policies are failing. A crisis, brought on by resource collapse or social conflict, often brings about widespread acknowledgement of management failure. Recognition of fundamental problems can lead to a period of experimentation, learning, and innovation. The resulting insights set the stage for a new round of policy development and the next adaptive cycle.

The adaptive cycle describes some factors that can impede experimentation by management agencies. Learning, by ecosystem experimentation or any other means, may be viewed as a threat to dogma or entrenched policy during the rigidly bureaucratic phase of the adaptive cycle. Symptoms of this phase include "command-and-control" management styles, diminished research and monitoring budgets, and the belief that science is mainly useful for enforcement and litigation (Holling 1995). Creative science will not be favored under bureaucratic management regimes. On the other hand, science can make crucial contributions during the reorganization phase of the adaptive cycle.

Even when agencies are receptive to learning and open to the prospect of new management policies, progress may be halting and inefficient (Table 12.3). Hilborn (1992) documents several factors that affect the capacity of management agencies to learn from experience. Informative experimentation may require a radical change in management for a period of time and conservative managers may view these changes as too risky. An urgent need for results could prompt manipulation of the ecosystem before adequate pretreatment data are collected. Without premanipulation data, the experiment cannot be interpreted and therefore no learning takes place. Lack of shared vision may lead to complex manipulations of many factors, which yield results that are hard to interpret. Useful ecosystem experiments change one aspect of an ecosystem in a strong sustained way, for a long enough time period to learn the consequences. The institution may be unable to maintain the experiment for the required time to learn from it (Hilborn 1992). Turnover of personnel, changes in political pressures, or unforeseen budget problems may cause an experiment to be abandoned or compromised before the objectives are achieved. Some of these limitations could be overcome by improvements in training that prepare agency personnel to take greater advantage of opportunities to learn by doing.

Institutional Limitations

Ecosystem experimentation is also limited by the kinds of institutional arrangements available to operate experiments. Institutional challenges include coordination of management personnel and scientists in ways that achieve overall objectives in addition to fostering individual creativity and

TABLE 12.3. Some barriers that can prevent effective management experiments.[1]

Barrier	Explanation	Solutions
Excessive bureaucracy	Learning perceived as threat to entrenched policy	Wait until the need for change is obvious
Excessive caution	Manipulations that would be informative are viewed as risky	Subdivide the resource and experiment with part of it; wait until the potential value of better management outweighs the risks
Manipulation is done too early	Premanipulation data are not sufficient to interpret the experimental results	Collect adequate premanipulation data; describe the system adequately before experimenting
Dithering	The manipulation is overly complex; too many variables are changed at one time	Change one aspect in a strong sustained way, for a long enough time period to learn the consequences
Learning disabilities	The institutional attention span is too short; the experiment is compromised before the ecosystem can respond	Sustain the experimental design a time period long enough to detect ecosystem responses

1. See Hilborn 1992; Gunderson et al. 1995.

productivity, the logistics of the experiment itself, and sustaining the program for the time period required to determine the ecosystem response and interpret the results.

One indicator of institutional problems may be the relatively narrow range of staff sizes associated with successful ecosystem experiments. If the research team is too small, the necessary disciplines cannot be included and the experiment will fail to meet scientific goals. If the research team is too large, the level of bureaucracy necessary to conduct the experiment can become excessive and obstruct creativity or even the integrity of the experiment itself. Schindler (1992) describes some pathologies that can arise in extremely large environmental research programs. Adaptive environmental management, which explicitly views management activities as experiments, may work best with small, flexible institutions (Lee 1992). Evidence from well-known, successful ecosystem experiments suggests that the optimum team size is approximately ten to thirty people (i.e. senior scientists and managers, plus essential technical staff, graduate students, and postdoctoral researchers). If this is true, it suggests that there may be a limit to the scope of successful ecosystem experimentation. Alternatively, we may need to devise innovative new management approaches that facilitate success of larger ecosystem experiments.

Progress from Ecosystem Experiments Can Be Accelerated

Ecosystem experiments are a nexus of growth for ecosystem science and management. Human pressures on the environment will grow for the foreseeable future and experimentation is an efficient way to learn the effects of human action and compare the consequences of alternative management policies. At the same time, large-scale management experiments can stimulate vital, relevant science (Slobodkin 1988).

It is surprising that so few management actions or developments are viewed as large-scale experiments. In truth, management plans are hypotheses masquerading as answers. Orians (1986) points out that every environmental impact statement is a hypothesis for which the necessary manipulation will be carried out. With postmanipulation monitoring and a reference ecosystem, every environmental impact study could be an ecosystem experiment. The same is true for planned timber harvests, fish stocking, toxin remediations, and so forth. Paine et al. (1996) suggest that coastal oil spills are opportunities for large-scale experimentation which, however tragic, should not be wasted. Of course, more proactive ecosystem experiments are also needed on a great number of questions. In the next sections, some actions are suggested that could accelerate progress through ecosystem experimentation.

Leadership

The best-known and most productive ecosystem experiments have been led by a handful of close colleagues (Likens chapter 10) and productive collaborations seem to owe as much to luck as to design. Because of this, ecosystem experimentation may be limited by the numbers of scientists willing and able to form the necessary teams. Additionally, graduate training programs should be modified to develop research styles suited to ecosystem experimentation. Training in the history, opportunities, and challenges of ecosystem experimentation is needed for both academics and agency personnel.

Ecosystem experiments have generally been shorter in duration than the careers of the lead investigators, however, there are many questions that will require longer-term experiments. For example, what are the effects of chronic inputs of contaminants on ecosystems? Planning for longer-term experiments will require that issues of succession in leadership and continuity of vision be addressed. Ecologists have rarely considered these challenges.

Sites

Dedicated sites for ecosystem experiments are rare. Not all ecosystem experiments need to be performed in experimental reserves; management experiments, for example, may be performed in areas accessible to the public. Experimental reserves should be used to perform experiments that are risky to the resources, involve hazardous substances that should not be released in areas open to the public, or investigate crucial basic questions of ecosystem science. We are running out of time to create and sustain experimental ecosystem facilities like Coweeta, Hubbard Brook, Konza Prairie, the Experimental Lakes Area, Risdalsheia, Rothamsted, and the University of Notre Dame Environmental Research Center. Even these existing sites will not necessarily be maintained in the future. Canada's Experimental Lakes Area, for example, has experienced severe cutbacks in recent years.

Funding

Funding, or rather the lack of it, limits ecosystem experimentation. It can be difficult to persuade granting agencies to fund the extensive pretreatment studies needed for successful experimentation. It can be difficult to sustain grants for the length of time needed to see slow ecosystem responses. At the planning stage, the time horizon necessary to answer the questions should be clearly stated. The funders should be committed to sustaining the experiment for the necessary length of time, and the scientists should be committed to ending the experiment when it is over.

Management agencies should greatly increase their participation in critical ecosystem experiments. In some cases, management agencies may fund ecosystem experiments in experimental reserves about topics in which basic and applied questions intersect. However, the greatest growth opportunity lies in management experiments to compare and ultimately improve policies. To succeed, such experiments require carefully constructed partnerships between management agencies and academic scientists.

Keystones for Adaptive Ecosystem Management

Ecosystem experiments are critically needed to improve environmental management practices and policies. Adaptive ecosystem management is the process of adapting policies to changing ecosystems and changing societal expectations (Holling 1978; Gunderson et al. 1995) and tracking the changes in ecosystems that result from alternative policies (in other words, ecosystem experimentation) is central to adaptive ecosystem management (Walters 1986; Lee 1993; Walters chapter 11). Research relevant to adaptive ecosystem management must be flexible enough to address emerging questions, yet stable enough to sustain the long-term observations required to learn about ecosystems.

There are tremendous opportunities in combining the capabilities of management agencies and academic institutions for adaptive ecosystem management (Kitchell 1992). Agencies offer management expertise and authority or responsibility for the sites to be managed, and can dedicate staff and funding for careful, consistent measurements over the relatively long-time horizons needed for some ecosystem experiments. Academics bring scientific expertise and the talents of students and postdoctoral researchers. Student and postdoctoral staffs can be mobilized quickly around emerging scientific questions, yet the individuals (unlike permanent agency staff) move on when the project is over. Recognizing the potential power of agency–academic collaborations, attendees of the Second Cary Conference in 1987 called for a "new partnership between scientists and resource managers" (Likens 1989). Ten years later, at the Seventh Cary Conference, this partnership still remains largely unrealized.

In a common model for the interaction of agencies and academics, the relationship is asymmetric and can easily become adversarial (Figure 12.4a). Society has very different expectations of management agencies (which are funded to maintain ecosystem services) and academic institutions (which are funded to educate people and create new knowledge). In theory, academics can become informed of management needs, propose research to an agency, and eventually perform research and provide findings to the agency. In practice, however, this interaction is often fragile.

Interactions between management agencies and academic institutions can break down in many ways, much as a nonlinear, unstable interaction between two populations in an ecosystem. Academics and managers have different professional goals that are brought about by the different goals of their respective institutions. Departure of a key individual, political interventions, budget shortfalls, discoveries inconvenient to entrenched policy, or unprecedented ecological events can break the linkage between agencies and academics. In ecosystems, potentially unstable interactions can be stabilized by keystone species, which hold in check some component that would otherwise destabilize the system (Paine 1969). What are the keystones that might stabilize the interaction of scientists and managers?

A system that could sustain agency–academic partnerships should include a keystone responsible for adaptive ecosystem management (Figure 12.4b). The keystone could be a well-placed individual, a unit of an agency, or a freestanding institution. Society would fund the keystone to assess the status of ecosystem services, anticipate surprise, compare the performance of alternative policies, and adapt research and management to the evolving state of the ecosystems and societal expectations. Management agencies and academic institutions must collaborate to propose adaptive management projects, and conduct the necessary management actions and research. Westley (1995) notes that power dispersal is essential to successful collaboration. The keystone model distributes power in a potentially stabilizing way.

The keystone also encourages academics and managers to develop convergent goals. They must work together to propose projects, satisfy review

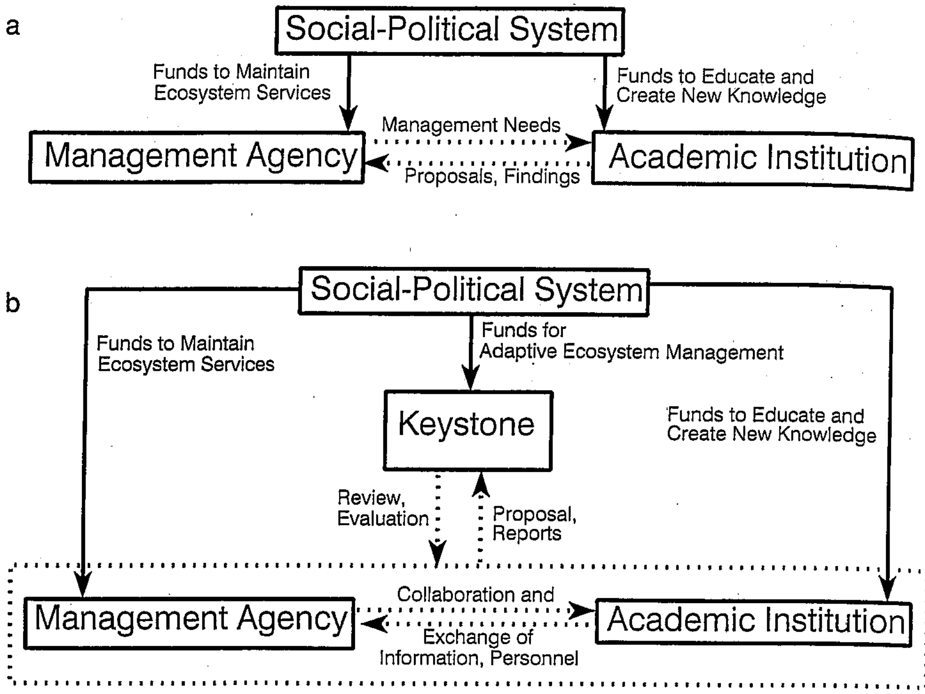

FIGURE 12.4. (a). A common model for the interactions of management agencies and academic institutions. (b). Proposed keystone model for interactions of management agencies and academic institutions.

and evaluation criteria, and achieve common goals of experimental management and scientific inference. Both management and academic institutions should reward individuals for writing successful proposals and publishing useful results and both institutions should thereby select personnel who are successful collaborators.

Are there examples of the keystone model? Case studies of ecosystem management (Gunderson et al. 1995) include a number of situations in which keystones emerged. In the Columbia River basin, the Northwest Power Planning Council was formed as a neutral institution responsible for system-wide decisions and coordination of diverse investigations (Lee 1993; McLain and Lee 1996). The International Joint Commission and the Great Lakes Fisheries Commission functioned as keystones at certain times in the management of the Great Lakes (Francis and Regier 1995).

Keystones may be short-lived, however. Westley's (1995) review of interorganizational collaborations implies that successful collaborations are often transient. She also notes advantages of informality:

> ... too much consensus and organization may make the interorganizational system vulnerable. For the actor in such systems, therefore, it is important to resist too much organization and centralization... Although the idea that policy should be treated as experiment is a brilliant one, it is difficult to achieve. Scientists should continue to be wary of politicians prepared to turn theory into policy. A healthy tension between the two, a redundancy of efforts and activities may offer the most fertile ground for individuals to manage the process of change. (Westley 1995).

Thus, the most effective keystone organizations may have short lifetimes relative to the constituent institutions and the ecosystems being managed. They are "ad-hocracies," not bureaucracies (Gunderson et al. 1995). For the ecosystem experimenter, this raises a dilemma. Informal collaborations may be the optimum for flexibility and creativity (McLain and Lee 1996), however, stable research arrangements (for years to decades) are essential to learn how ecosystem processes respond to management interventions.

Successful examples of ecosystem experimentation and adaptive ecosystem management show that both are possible. But these successes may be a consequence of happenstance collaborations and the dedicated leadership of a few individuals. In other words, luck seems to be involved. Can we create circumstances that increase the frequency of successful ecosystem experiments and adaptive policy design? If so, we can break a critical bottleneck that limits ecosystem experimentation.

People and Nature

Humans are now the dominant species of Earth's ecosystems. Ecologists can no longer study nature separately from people, and in fact many ecosystem studies do measure human impacts. Humans have appeared as independent variates or covariates in many ecosystem studies (McDonnell and Pickett 1993), including a few ecosystem experiments (Kitchell 1992; McAllister and Peterman 1992; Walters 1993). However, to my knowledge no ecosystem experiments have explicitly included people or institutions as *dependent* variables. When human response has been studied in ecosystem experiments, their behavior has always created surprises for ecologists. Some of the best examples come from fisheries. Hilborn et al. (1995) note that "... the biggest failure in natural resource management has been the widespread neglect of the dynamics of the exploiters." They point out that commercial fishing regulations have almost universally failed to control exploitation in the ways expected by scientists and managers.

These experiences point to a need for ecosystem studies, including experiments, that address people and nature as an interacting system (Folke chapter 13). Human activity changes ecosystems, and the altered ecosystems prompt change in human behaviors, economies, and institutions. For example, Likens (1992) describes "leapfrog degradation" of lake districts. As cabin sites develop around lake shores, riparian vegetation is removed, and fishing and water quality decline and consequently, a better view of the lake makes the lake less desirable to view (Kitchell 1992). Development activity then shifts to other, more remote lakes. Such feedbacks are rarely studied by ecologists, yet the effect of a changing environment on human attitudes and behavior toward the environment is surely one of the most potent ecological forces on the planet.

Ecosystem experiments that view people as interactors with nature (i.e. as both dependent and independent variates) will require new collaborations of ecologists and social scientists. It will take concerted effort to build these cross-disciplinary links. Pioneering collaborations of social and natural scientists suggest some exciting lines of inquiry but also point to significant conceptual, methodological, and empirical problems (Costanza 1991; Gunderson et al. 1995; Hanna et al. 1996; Folke chapter 13). We must find ways to improve environmental management using large-scale experiments that integrate the dynamics of humans and ecosystems (Lee 1993; Gunderson et al. 1995). To succeed, we must carefully describe the systemic context of these experiments: conceptual, temporal, and spatial. Theory, long-term studies, and comparisons have provided crucial context for ecosystem experiments to date, and will continue to do so in the future. Building an ecosystem ecology that includes Earth's dominant species as an interactive component, not an external component, will require the tools that have served us well in the past, plus novel and surprising ones that may arise from new cross-disciplinary work.

Acknowledgments. I thank Tom Frost, Jim Kitchell, and Mike Pace for years of dialogue about ecosystem experiments. Opportunities to learn by doing have been provided by the University of Notre Dame Environmental Research Center and the Wisconsin Department of Natural Resources (WDNR). Several colleagues at WDNR, especially Jim Addis, Paul Cunningham, Doug Knauer, Dick Lathrop, and Mike Staggs, have influenced my thinking about ecosystem experiments. Gene Likens offered insights about rationales for ecosystem experiments and Gordon Orians shared his views on environmental impact assessment. Participants in a planning workshop at the National Center for Ecological Analysis and Synthesis provided very useful reviews of an early outline. Helpful comments on the draft came from Nina Caraco, Stuart Fisher, Tom Frost, Bob Hall, Jeff Houser, Jim Karr, Conrad Lamon, Dick Lathrop, Tara Reed, Bill Robertson, Daniel Schindler, Gaius Shaver, and Kathy Webster; this does not imply that they agree with everything I have written. I am grateful for the support of the National Science Foundation, the Andrew W. Mellon Foundation, and the WDNR.

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