Ecosystem Experiments

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Experimental manipulations of entire ecosystems have been conducted in lakes, catchments, streams, and open terrestrial and marine environments. Experiments have addressed applied problems of ecosystem management and complex responses of communities and ecosystems to perturbations. In the course of some experiments, environmental indicators and models have been developed and tested. Surprising results with implications for ecological understanding and management are common.

Predicting responses of ecosystems to perturbation is among the greatest challenges to ecology. Experiments are necessary, yet many important features of ecosystems, such as wide-ranging predators or large-scale geochemical processes, cannot be included in small artificial systems. Other features, such as microbial metabolism or plankton populations, quickly reach unrealistic levels when isolated in containers. Such difficulties are overcome by direct experimental manipulations of entire ecosystems, including the organisms and the abiotic environment (*1*). These experiments involve large areas, such as catchments or the natural ranges of mobile predators, for extensive periods of time (Fig. 1).

Ecosystem experimentation is field science. The outdoor laboratory may not be replicable, is not controlled, and is subject to many fluctuations. Experimental design usually involves trade-offs of spatial extent, replication, and duration, all constrained by financial resources. Challenges include the possibility that changes in experimental ecosystems are the result of historical trends or regional patterns rather than the manipulation. The value of unmanipulated reference ecosystems as a check for such problems has long been recognized (*2*). Ideally, long-term pre- and postmanipulation data are gathered for several reference ecosystems. Experimental systems should be monitored for long enough to assess trends before treatment (*3*).

Manipulations are usually simple, direct, and sustained for long enough to detect changes against background variability. Natural perturbations and management actions can be multifactored, modest, or brief and consequently their effects are hard to interpret (*4*). For example, changes in harvest regulations that are too small to have detectable effects are a major source of uncertainty in assessments of fishery management practices (*5*). Informative manipulations are simple and powerful.

Replication is often impossible because of costs, public policy, or uniqueness of the ecosystem to be studied. Ecosystem experiments are more often intended to measure responses and their ecological significance than to test null hypotheses and their statistical significance (*6*). Generalization beyond a single system depends on knowledge of mechanisms or comparisons of many ecosystems. Repetition of important experiments by diverse research groups is a valuable check on the generality of responses. For example, similar ecosystem experiments have been performed in several nations on lake eutrophication, lake biomanipulation, ecosystem acidification, and effects of forest management on catchment hydrology and biogeochemistry. Comparison of independent experiments reveals which conclusions are general and which depend on local conditions (*7*).

From origins in limnology (*8*), whole-ecosystem experimentation has been applied to diverse habitats. Initial work focused on biogeochemistry and chemical stressors of ecosystems, but the scope has expanded to include community dynamics and interactions of community and ecosystem processes.

Terrestrial Ecosystems

Catchments are basic units of the landscape (*9*, *10*). Because boundaries can be well-defined, fluxes of water and chemical components can be measured into and out of the ecosystem. Atmospheric inputs include gases, particles, water, and dissolved chemicals. Water passes through the terrestrial ecosystem, and is thereby altered in chemical composition in ways that can be attributed to known biological and geochemical processes. Runoff from catchments thus integrates the net effect of terrestrial processes. Changes in the amount and composition of runoff reflect changes in atmospheric inputs or in the terrestrial ecosystem.

The paired-catchment concept is central to whole-catchment research. Typically, runoff is compared from two ecosystems. After a pretreatment study, one catchment is manipulated while a second serves as untreated reference.

In a classic experiment at Hubbard Brook Experimental Forest, trees were cut and regrowth was inhibited by administration of herbicide, while a reference catchment was undisturbed (*9*). This manipulation drastically altered hydrologic flows, erosion, and biogeochemical cycles for several years. Extensive nutrient loss resulted from decomposition and nitrification. The experiment showed the tight linkage between terrestrial ecosystems and downstream aquatic ecosystems. It also led to specific recommendations of tree harvest practices that would maintain water quality, wildlife habitat, and productive potential of forests (*11*).

Paired catchments (or paired forest stands) have been used to investigate other environmental processes. The effects of acid deposition on surface water have been revealed by large-scale experiments. Among these is the RAIN (Reversing Acidification in Norway) study of the effects of acid deposition on soil and runoff chemistry (*12*). Exclusion of acid rain from a whole catchment by means of a roof showed that the effects of acid inputs were reversible (Fig. 1A). A parallel experiment with increased inputs of acids to a pristine catchment showed that surface waters could be acidified after only a few years of acid deposition (Fig. 2). As a scientific experiment, the RAIN project revealed mechanisms and rates of change of runoff and streamwater chemistry after changes in inputs of acidic pollutants (*13*). As an environmental demonstration, the RAIN project showed that acidification of surface waters was due to acid deposition and that acidification could be reversed when this deposition was reduced. These experiments expanded into manipulations of coupled catchment-lake ecosystems and studies of liming and other measures to mitigate acidification (*14*).

Concern about the effects of global change on ecosystems has led to new experiments. Facilities of the RAIN project have recently been converted to examine effects of elevated CO_2 concentration and temperature on catchments (*15*). Increased atmospheric CO_2 concentrations and N deposi-

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tion are expected to increase forest growth and sequestration of C, whereas increased temperature should stimulate soil respiration and loss of C, so the net effect on the global C budget could be either positive or negative (*16*). Large-scale experiments are the only realistic means of answering this question.

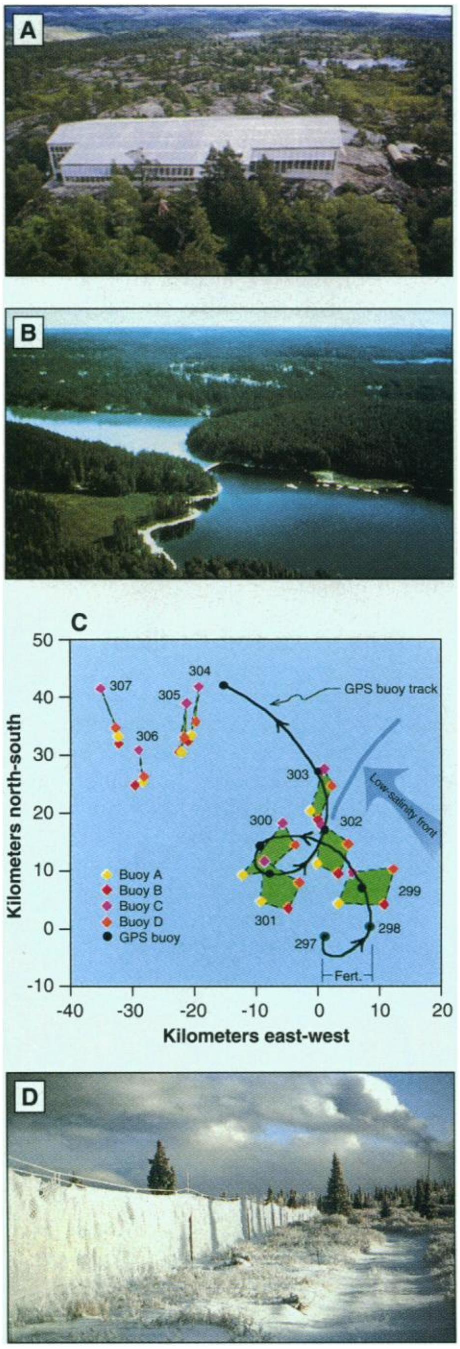

Fig. 1. Ecosystem experiments. (**A**) Enclosed headwater catchment at Risdalsheia, Norway. (**B**) Lake 226 at the Experimental Lakes Area, Ontario, was partitioned at the constriction. In the far basin, fertilized with inorganic P, N, and C, algae bloomed within 2 months. No increase in algae occurred in the near basin, fertilized with only C and N. [Photo: D. Schindler] (**C**) Movements of a 64-km^2 patch of Fe-fertilized water (green tetragons) during days 297 through 307 of 1993 in the equatorial Pacific Ocean. (**D**) Electric fence on 1-km^2 predator exclosure, Kluane Lake, Yukon. [Photo: K. Hodges]

Freshwaters

Freshwater ecosystem experiments have addressed the responses of both communities and biogeochemical processes to a wide variety of environmental stresses. The relative ease with which lakes can be studied by small teams has yielded some of the best examples of ecosystem experiments. Manipulations of lakes have been used to study the effects of nutrient enrichment, acidification, alkalization, methane addition, the biogeochemical fates of radioactive materials and toxins, reservoir formation and linkages between acidification, climatic warming, and ultraviolet exposure (*2, 17–19*). Ecosystem experiments in streams have manipulated riparian vegetation, pH, nutrients, and litter input (*20*).

Results from whole-lake experiments have refuted the idea that eutrophication could be prevented by low carbon concentrations (*21*). Nutrient budgets and gas exchange measurements showed that the necessary C invaded lakes from the atmosphere at rates sufficient to support algal blooms (Fig. 1B). This gas flux, prevented in bottle experiments and forgotten in nonexperimental studies, proved crucial in ecosystem experiments. Subsequent whole-lake experiments showed that N also could be drawn from the atmosphere, after establishment of cyanobacterial blooms (*22*). These experiments showed that eutrophication could be controlled by managing P alone, setting the stage for P control legislation in North America and Europe.

Surprising biological responses have occurred in many aquatic ecosystem experiments. For example, whole-lake acidifications showed that impacts were transmitted through food webs to affect populations of fishes and aquatic birds (*19, 23, 24*). Ecosystem manipulations have changed foraging and predator-avoidance behaviors of fishes within days, causing indirect effects that cascade through food webs to alter productivity and nutrient cycling (*25, 26*).

The biota also affect the resistance of lakes to acidification (*27*). Lake acidification experiments showed that H^+ was consumed by microbial denitrification and sulfate reduction, and that neutralization was increased, not diminished, by inputs of sulfuric and nitric acids (*28*).

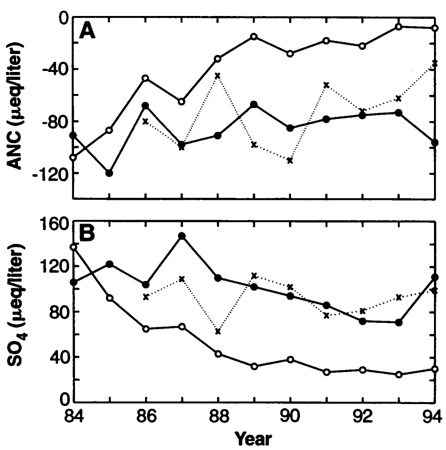

Fig. 2. Volume-weighted concentrations of (**A**) acid-neutralizing capacity (ANC) and (**B**) sulfate in runoff from a roofed catchment receiving acid rain (●), an unroofed catchment receiving acid rain (X), and a roofed catchment receiving clean rain (O) during 1984 to 1994 (*12*).

Oceans

Oceanographers have used an unenclosed ecosystem experiment to answer a puzzling question: Why do vast regions of the oceans have high concentrations of N and P (usually thought to limit productivity) yet low phytoplankton biomass? One hypothesis among several (*29*) is that phytoplankton of these regions are limited by Fe (*30*). The Fe hypothesis has proven impossible to address unambiguously in bottle experiments, because corrections for zooplankton grazing are difficult (*31*) and the probability of contaminating the bottles with trace amounts of Fe is high (*32*). To overcome these limitations, the first unenclosed open ocean fertilization experiment, IRONEX, was performed in the equatorial Pacific (*33*). Dissolved Fe was added to an unenclosed 64-km^2 patch of water to elevate the ambient concentration 100-fold. The patch was tracked with a drogued buoy, and the inert tracer SF_6, added with the Fe, was used to monitor the geometry of the patch (Fig. 1C).

The biological response to the Fe enrichment was surprisingly rapid. Photosynthetic efficiency increased within the first 24 hours (*34*), and by the third day chlorophyll concentration and primary productivity had tripled. Increased photosynthesis caused a small but significant drawdown of CO_2 in the surface waters (*35*) but was not sufficient to cause detectable decreases in nutrients.

Although the results of this first oceanic ecosystem experiment are encouraging, many questions remain. It is not clear whether the modest productivity increase and negligible impact on N and P levels resulted from the disappearance of available Fe, increased zooplankton grazing, or the short duration of the experiment. An experiment is planned to address these alternative explanations, in which a patch will be repeatedly fertilized with Fe and sampled for a longer period of time. Zooplankton abundance and grazing rates will be monitored, thus determining whether herbivores mitigate the response of phytoplankton to Fe.

The issue of whether Fe additions can cause extensive phytoplankton blooms in the oceans has significant implications for environmental policy. It has been suggested that fertilization of the entire Southern ocean with Fe could sequester substantial quantities of atmospheric CO_2, delaying predicted greenhouse warming of the earth to a significant, but modest, degree (*36*). Debates about the feasibility, wisdom, and ethics of such climate engineering have been greatly handicapped by our limited knowledge of the response of oceans to nutrient enrichment (*37*). Only through experiments like IRONEX can our understanding be expanded sufficiently to inform the decision-making process.

Food Webs

Ecosystem experiments are well suited to investigations of wide-ranging or long-lived populations. Limnologists have tested the idea that food web manipulation can control nuisance phytoplankton growth. Phytoplankton are consumed by herbivorous zooplankton, and the most effective herbivores are preferred prey of zooplanktivorous fishes (Fig. 3, inset). To increase grazing, experimenters have removed zooplanktivorous fishes, or added piscivorous fishes that eat zooplanktivores (*26, 38*). Where planktivorous fishes are abundant, large, herbivorous zooplankton are absent and phytoplankton respond strongly to P enrichment (Fig. 3). Where piscivorous fishes exclude planktivores, large herbivores flourish and reduce the response of phytoplankton to P enrichment (*39*). Such experiments show that biomanipulation of food webs can reduce eutrophication.

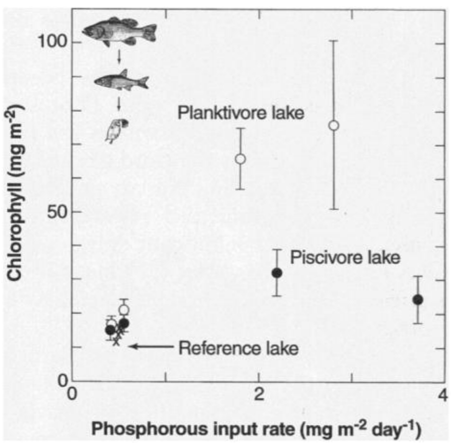

Fig. 3. Phytoplankton chlorophyll (July, mean ± SE) versus P input rate in an unmanipulated Reference Lake (X), a Piscivore Lake (●), and a Planktivore Lake (O) (*39*). Key links in the food web (inset) are piscivory by bass (*Micropterus* spp.) on planktivorous golden shiners (*Notemigonus crysoleucas*), which prey on large zooplankton herbivores (*Daphnia* spp.). Large herbivores are abundant in the Piscivore Lake and absent in the Planktivore Lake.

Manipulation of dominant herbivores in terrestrial food webs has also shown dramatic effects. For example, moose exclosures on Isle Royale caused major changes in plant composition, production, and nitrogen mineralization (*40*).

Manipulations of vertebrate predators, however, have been attempted only recently in terrestrial ecosystems. Boreal forests of North America support a community of vertebrates that fluctuate in a 10-year cycle (*41*). In 1986 a 10-year experiment was undertaken to manipulate nutrients, herbivore food supply, and predation in 1-km^2 blocks of white spruce forest, while the dynamics of the six major prey species and five major predator species were analyzed (Fig. 1D) (*42*). Nutrient addition had little effect on hare numbers, even though plant growth responded dramatically to nutrients (Fig. 4). Both artificial food addition and predator reduction increased hare density, especially in the decline phase of the cycle. The combined effects of food addition and predation reduction were very strong when hares were declining. This response may involve risk-sensitive foraging by hares, which respond to high predator numbers by using habitats with more cover but less food (*43*). However, the entire vertebrate community is not controlled by predation. Red squirrel, vole, and mouse populations respond primarily to their food supplies, and predation is unable to control their numbers from year to year (*44*).

Indicators of Ecosystem Change

Ecosystem experiments help determine indicators of environmental change. These indicators can then be followed in monitoring programs or used to reconstruct changes from historic records. Paleolimnologists have used long-term, whole-lake experiments to calibrate sedimentary indicators of food web change and eutrophication (*45*). Indicators included zooplankton remains that reveal herbivore assemblages and carotenoids and diatoms that reveal phytoplankton dynamics.

Population responses are generally more sensitive indicators of stress than ecosystem responses (*46*). For example, lake acidification eliminates fish reproduction and sensitive invertebrate species at pH 5.6 to 6.1, whereas primary production is unaffected even at pH 4.5 (*18*). This surprising discovery has implications for environmental monitoring and for concepts of the linkage between populations and ecosystems. Ecosystem process rates are stabilized by replacement of sensitive species with tolerant ones that perform similar ecosystem functions (*47*). Thus, obvious changes in populations can occur at levels of stress that have little effect on ecosystem functioning, when impacts of stress may be reversible. Severe or irreversible damage may have taken place by the time significant change occurs in ecosystem processes (*18*).

Results of large-scale experiments are vital for evaluation of predictive models (*5*). Such models are among the few tools available for anticipating effects of global change and more local perturbations. For example, acidification experiments have provided independent tests of models that are now widely used to determine critical levels of acid input for soils and freshwaters (*48*).

Because ecosystem experiments cannot be performed for every ecosystem and every stress, most ecosystems will be monitored and managed by means of indicators and inexpensive bioassays. Ecosystem experiments are the most direct means of calibrating indicators against known perturbations at the actual scale of environmental impacts.

Prospects and Applications

Ecosystem experiments are a powerful method for evaluating and predicting impacts of environmental change. These experiments have revealed how diverse ecosystems respond to physical, chemical, and biotic perturbations. Direct tests of key ecological ideas will continue to be an important use of ecosystem experiments.

Results of ecosystem experiments are highly relevant to environmental policy. There are many opportunities to expand the role of large-scale, long-term interdisci-

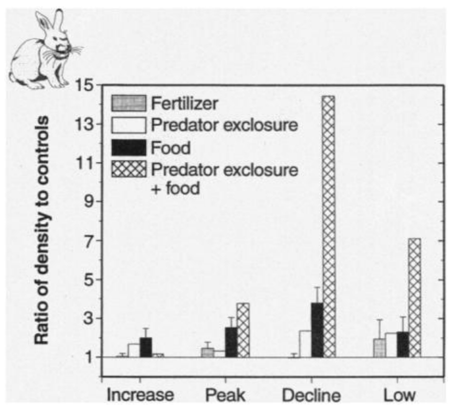

Fig. 4. Mean responses of snowshoe hare (*Lepus americanus*, inset) populations to manipulations during the four phases of the 10-year population cycle at Kluane Lake, Yukon (*42*). Predator exclosures exclude mammalian, but not avian, predators. Food was supplied year-round as commercial rabbit Chow. Fertilizer was added as N, P, and K.

plinary experimentation in adaptive management of ecosystems (49). Many management actions are unplanned experiments from which we could learn a great deal if appropriate pretreatment data, reference ecosystems, and monitoring programs were implemented. However, experimentation in the context of management can be difficult (49). For example, policy may dictate manipulations that are too small to have detectable effects, or multifaceted manipulations with effects that are hard to separate. The greatest progress has occurred when straightforward experiments are performed by relatively small interdisciplinary groups cognizant of the relevant management and scientific issues.

Effective experimentation at the scale of management requires dedicated sites with sustained funding. Such sites, which are now rare, are needed to conduct selected ecosystem manipulations, provide long-term data for evaluating environmental change and management actions, and develop the indicators and basic understanding necessary to manage ecosystems. Sites are needed in a diversity of terrestrial, freshwater, and marine habitats where human activities can be an important cause of ecosystem change.

Ecosystem experiments are the most direct method available for improving predictions of environmental response to management or inadvertent perturbation. For this reason, we believe that large-scale experimentation will make increasingly important contributions to the scientific basis of ecosystem management.

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