

Scientific Accomplishments of the Long Term Ecological Research Program: An Introduction

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On the premise that today's complex environmental challenges require innovative long-term study over many types of habitat and over large areas of the landscape, the National Science Foundation established the Long Term Ecological Research (LTER) Network. The LTER Network consists of 24 sites located throughout the climates and habitats of North America and Antarctica. Although the scale of research and specific research foci differ across sites, the LTER sites share a commitment to the long-term perspective and to measurements that extend over decades. Researchers at these sites study many species and environmental variables, from bacteria to bison and from air temperatures to soil moisture. Synthetic results include an analysis of the relationship between diversity and productivity in multiple ecosystems; a model of the workings of an entire ecosystem at one site; and a compilation of regional effects of changes in temperature, precipitation, and nitrogen deposition. Sites are funded for 6 years at a time, with the expectation that continued high-quality research will lead to a decades-long project.

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How and why is the Long Term Ecological Research (LTER) Network's approach to ecological studies different from that of other networks? One difference is that each LTER project has the opportunity to choose its own research focus. The result is a wide variety of topics and projects that take advantage of the diverse habitats around the research sites and the diverse scientific skills of the research teams and participating institutions. Strong scientists remain on the projects, attracted by opportunities for multidisciplinary research, synthesis, and experimental manipulations that may last 20 years or more. Yet these opportunities for diversity are balanced by commonalities across sites that result from their belonging to the LTER Network. One requirement for inclusion in the network is that all data must be available on the Internet. Another is that every site should include research on some of the five LTER core research areas, which include primary production, decomposition, and disturbance (see table 1 in Hobbie et al. 2003). This ensures that all sites carry out a broad range of research and that comparisons among sites are possible. Moreover, comparisons and syntheses across sites are actively encouraged through the availability of small grants to measure a process at a number of locations that might include both LTER and non-LTER sites. In addition, cooperative and comparative research is a requirement for renewal of each LTER project; proposal reviews take into account the amount of cooperative and comparative research to be produced.

Another major difference between the LTER Network and other networks is the structure of the LTER program.

Once NSF holds a competition and a panel selects a site for funding, continuation for an LTER project is judged every 6 years by a panel whose criteria include scientific progress; quality of publications, management, and education; and degree of cooperative work with other sites. After the initial competition, sites no longer compete against one another for continuation. Equality of resources and a fundamentally cooperative attitude among sites are now basic characteristics of the LTER program.

The LTER statistics are impressive. More than 1200 scientists take part in the network. There are educational programs for grades kindergarten through 12, for undergraduates, for graduate students, and for postdoctoral fellows. Twelve thousand LTER-related journal articles were published from the start of the program in 1980 through 1995. Seven books, each of which synthesizes research at separate sites, have been published, and 13 more are in preparation. There is a cooperative program with international LTER programs in more than 20 countries; most of these programs were modeled after the US LTER Network. Thousands of data sets are available on the Internet. On average, each LTER site leverages its NSF funding threefold.

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There is no doubt that the LTER program is producing publications, graduate students, and data (Hobbie et al. 2003). But what has the LTER program contributed to the intellectual progress of ecological and environmental sciences? This special section takes direct aim at this question. The 36 authors focus on the accomplishments of the LTER program in six areas of ecological research. These themes, which were chosen to encompass research at many of the sites, cover some but by no means all of the LTER research. Authors have included mainly LTER-associated results instead of aiming for an exhaustive review of the literature on a particular theme. In many cases the unique features of the LTER project and the sites made the research possible.

Past, present, and future long-term research

The central, organizing intellectual aim of the LTER program is to understand long-term patterns and processes of ecological systems at multiple spatial scales. The programmatic challenge faced by the LTER Network is fostering this central aim while maintaining the site diversity and independence that keep the quality of the projects high. However, despite the habitat diversity of 24 sites in freshwater, marine, estuarine, forest, grassland, desert, urban, and agricultural locations, many of the site questions and foci overlap (table 1 in Hobbie et al. 2003). For example, 11 sites list the topic “climate forcing and climate change” as an important focus. In addition, notwithstanding the great habitat diversity and hence the variety of site topics, the number of ecological processes to be studied are limited. The controls of these processes have many basic similarities worldwide, as is evident from the success of the Long-Term Intersite Decomposition Experiment Team (LIDET), which determines the effects of substrate quality and macroclimate on decomposition at 17 LTER sites (Kratz et al. 2003). The LIDET project has resulted in an understanding of how this fundamental process operates under different environmental conditions.

Ecological processes and present species assemblages cannot be understood in isolation. It is now clear that every system is undergoing long-term change and that long-term changes can only be studied with long-term measurements. As explained by Turner and colleagues (2003), LTER projects can monitor and lead to understanding of slow events, and also of the infrequent events that are often important shapers of ecosystems. The LTER data sets are now extensive enough to provide valuable predisturbance baseline data for the biota of a lake before an invasion of two new species, for example, or for the productivity of a tropical forest before a hurricane.

LTER sites are a valuable focus for long-term research activity. Hobbie and colleagues (2003) liken the network to a fleet of research vessels in oceanography, where the concentration of expertise, technical capability, and quality of data attract diverse research projects. They conclude, “Collocation of research projects makes efficient use of costly data and long-term experimental manipulations; it also increases the possibilities for creative breakthroughs from interdisciplinary collaboration” (p. 27).

Climate forcing and ecological interactions

The network of LTER sites includes over 80% of the possible climate types of North America (Köppen classification; McKnight 1999). While climate measurements take place at every site, LTER climate research takes advantage of the long-term database of ecological change at each site, as well as the detailed research on processes to determine the links between climate and ecology (Greenland et al. 2003). Some LTER climate research takes place at sites rarely sampled by national weather observing systems. For example, research from the Palmer Station LTER site in Antarctica documented the effects of stratospheric ozone depletion on planktonic algae.

Site-based research often serves as an incentive to expand scales of research. The detailed data on topography and climate at the Shortgrass Steppe site led to explanations of the reasons for differences in the greenness of the region as seen by satellite sensors. At the North Temperate Lakes site in Wisconsin, data were collected originally to construct a long-term record of ice freeze and breakup on a single lake. As a result of changes found, Magnuson and colleagues (2000) expanded the database to document a proxy for similar climate variations in several parts of the Northern Hemisphere.

The dynamics of ecosystems cannot be decoupled from atmospheric processes. While the effect of the atmosphere on ecosystems is well studied, Greenland and colleagues (2003) document the relatively new concept that ecosystems are an integral component of the atmospheric processes. For example, vegetation helps modulate temperatures in the lower atmosphere through the release of gaseous and particulate hydrocarbons (Hayden 1998).

Land use and its legacies

There is growing recognition that virtually every ecosystem on Earth is influenced and even shaped by legacies of past land use (Foster et al. 2003). In North America the present ecology of the Yucatán Peninsula of Mexico can only be interpreted through knowledge of Mayan land use a thousand years ago. Eight LTER sites in the eastern United States reflect a history of early settlement, intensive logging, and widespread agriculture followed by decline in land-use intensity and by reforestation. Detailed studies reveal impacts on forest structure and composition, and soil properties changed by the loss of soil horizons and the reduction in soil organic matter. There are also interactions with natural disturbances. For example, Hurricane Hugo's impact on Puerto Rican forests corresponded more to 19th-century land use than to the velocity of the wind that led to the blowdown.

Implications of past land use must be considered for sound management of natural resources. At the Konza Prairie LTER site, long-term experiments reveal effects of bison or cattle grazing, fire, mowing, and nonmanagement. Fire enhances nutrient mineralization and productivity, but bison grazing is necessary to maintain high biodiversity.

A goal of conservation is often restoration of the ecosystem to some previous condition. Often this condition may have been culturally maintained by fire or grazing. Without a full

understanding of the forces and processes that shaped past systems, restoration will be empirical and more miss than hit.

Disturbance dynamics and ecological response

Disruptions of ecosystems, communities, or populations that change resources, substrate availability, or physical environments are a part of nature. A variety of important ecological disturbances occur across the network of LTER sites, including hurricanes along the East Coast and in Puerto Rico, crown fires in Alaska, grazing in prairies and desert sites, and forest harvest in eastern and western forests (Turner et al. 2003). Responses vary from increasing spatial heterogeneity to upsetting ecosystem equilibrium on a large scale. Disturbances both create and respond to spatial heterogeneity, and they maintain ecologically important dynamics in ecosystem structure and function.

LTER data provide a valuable baseline against which to detect slow changes and measure ecosystem response to disturbance. For example, events such as the invasion of a non-native species of crayfish in Wisconsin lakes and resultant ecosystem changes have been detected only because of regular long-term measurements. Sudden catastrophic events also provide fundamental ecological information. As a result of LTER data collected before and after Hurricane Hugo in 1989, the understanding of tropical forest dynamics has changed. Before Hugo, the forest was thought to be fragile; after Hugo, LTER data showed it to be resilient.

Ecological understanding needs to go beyond a focus on single disturbances and single-species responses. At the Konza LTER site, both fire and grazing are under study. At other sites the response to drought can best be examined by taking advantage of the synoptic understanding available at LTER sites.

Biodiversity and ecosystem function

The number and kind of species present determine the specific traits represented in an ecosystem (Symstad et al. 2003). Species diversity, therefore, affects ecosystem processes. Present-day losses in species diversity make it increasingly urgent to understand how diversity affects ecosystem functioning and vice versa. The LTER Network is crucial to understanding the implications of the loss of biodiversity worldwide. Not only does the network provide long-term measurements of community change in a variety of habitats, it also allows long-term experimentation with ecosystems.

The suite of observations available at LTER sites allows cross-site studies of biodiversity. For example, Gross and colleagues (2000) studied the relationship between diversity and productivity of similarly structured herbaceous communities at six LTER sites. There were significant unimodal relationships (hump-shaped curves) at the scale of all grasslands or all of North America. But there were no significant relationships within any one biogeographic region, such as grassland or alpine tundra. The authors concluded that the spatial scale of analysis can influence the form of the relationship between diversity and productivity.

LTER sites are at the forefront of ecosystem manipulations that allow direct measurement of effects of diversity on ecosystem processes. Different approaches for manipulating diversity, including adding or removing species from existing communities and creating synthetic communities, have yielded different insights into the effects of diversity loss and the mechanisms behind them. In addition, experiments at LTER sites reveal the relative effects of biotic versus abiotic factors on ecosystem processes—a step toward answering the important question of the relative effects on the sustainability of ecosystem functioning of biodiversity loss compared with climate change, carbon dioxide enrichment, and habitat fragmentation.

Ecological knowledge from variability in space and time

Correlations of the responses of organisms with the year-to-year and place-to-place variability of natural systems yield valuable information about ecological relationships (Kratz et al. 2003). Long-term observations over many years or decades and at different scales are the key.

Analysis at a single site, the Arctic Tundra LTER, made use of the striking year-to-year variability of the summer climate. Some summers at this site are warm and dry, some wet and cold, and some a combination. This variability is reflected in the temperature and discharge of rivers at the site, where fish (arctic grayling) grow only during the 2-month summer. Careful observations of the annual growth of individual fish—more than 10,000 were tagged—allowed multivariate analysis of water temperature and discharge as controls of growth.

The LIDET experiment studied a single process across the entire range of temperature and moisture differences in LTER sites from the Arctic to the Tropics. In this 10-year experiment, leaf litter, incubation periods, and analytical methods were standardized. Extensive sampling tested the degree to which substrate quality and climate control the long-term carbon and nitrogen dynamics of decomposing leaf and fine root litter.

Long-term detailed data at the LTER Shortgrass Steppe site allowed researchers to test the assumption that responses at one site may be used to predict changes over an entire region. The 52 years of measurements of annual net primary productivity (NPP) were directly related to changes in annual precipitation. The resulting model was different from one that had been developed to explore the response of NPP to precipitation, which used data collected at sites across a much larger region of grassland. In other words, the models derived from temporal data did not agree with those developed from spatial data. Explanations are linked to the responses of vegetation distribution and biogeochemical processes to long-term or average conditions versus short-term variability.

These and other examples of the ecological use of long-term and large-scale data sets illustrate how the LTER program addresses ecological questions in ways that had previously not been possible.

Estimates of ecosystem properties across space and time

Models of ecosystem properties can be constructed on the basis of a mechanistic understanding of processes (Rastetter et al. 2003). This approach contrasts with the empirical approach described by Kratz and colleagues (2003), in which the correlation between ecological processes and a physical property is determined.

Models based on a mechanistic approach make use of the vast store of knowledge, derived from many studies, on processes underlying ecosystem function. Much of this information has come from LTER sites or from the sites of the International Biological Program (IBP) that predate the LTER (e.g., the H. J. Andrews Experimental Forest in Oregon, now an LTER site). This information on interactions and mutual constraints among ecological processes is then simulated with mathematical models. Knowledge of each process incorporates measures and experiments made over a wide range of environmental conditions. For this reason, the modeling results can be extrapolated in space and time with some confidence. The models can be used to predict broader-scale properties of ecosystems or whole regions. Examples are given here of spatial and temporal predictions of a model of photosynthesis over an Arctic watershed, of the spatial interactions among species of perennial grasses at three LTER grassland sites, of land–atmosphere interactions at the Short-grass Steppe LTER, and of forest properties in New England based on the long-term measurements of ecosystem function at the Harvard Forest and Hubbard Brook sites.

Mechanistic modeling is an important way to synthesize the understanding developed by ecologists. It is particularly valuable when the understanding can be tested by comparing the modeling results with experiments, with changes over time, or with spatial variation. Rastetter and colleagues (2003) make the point that the LTER program's data sets and approaches produce a depth of knowledge that is vital for scaling ecological processes across space and time.

Long-term ecological research and the ecological community

This special section of *BioScience* brings the contributions of long-term ecological research to the attention of the ecolog-

ical research community. Clearly the LTER program has made important contributions in many areas, a sampling of which are described here. Yet the LTER program offers additional benefits to ecological research in the form of baseline data with which research results from shorter-term studies in many subdisciplines and geographical regions can be compared. In its third decade, the LTER Network has reached a new maturity that encourages outreach to non-LTER ecologists and to scientists in related disciplines. Thus, this special section also serves as a call to those scientists to engage with the LTER program in synthesis and extension of the rich intellectual and data resources to help answer the urgent and intriguing ecological questions of the day.

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