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Long-Term Ecological Research and Network-Level Science

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With every passing year, the effects of global environmental change are becoming more pervasive and are occurring at a more accelerated pace. Climate change, land use change, atmospheric nitrogen deposition, ocean acidification and sea level rise, loss of biodiversity, and homogenization of Earth's ecosystems are all manifestations of human activities. These short- and long-term effects of environmental changes continue to mount.

In this time of heightened public awareness of, and concern about, how human activities are affecting our world, tools such as general circulation models and ecosystem process models can be used to predict the consequences of global environmental change.

Imagine if we also had the ability to track how a wide range of ecosystems was responding to global changes in real time. This predictive tool would be particularly powerful if it coupled multiple decades of information about ecological responses to environmental change with large-scale, long-term experiments and models from dozens of different ecosystem types.

In fact, this tool exists: It is the Long-Term Ecological Research (LTER) Network, which will soon celebrate its 35th anniversary.

The Foundation of LTER

The U.S. National Science Foundation (NSF) has funded LTER since 1980, but the foundations of the program can be traced back to the International Geophysical Year (IGY; 1957–1958). Ecologists were impressed by the success of the IGY, from which they conceived and initiated the decade-long International Biological Program (IBP; 1964–1974). The IBP marked a significant increase in research funding for ecosystem science and is credited with the establishment of "big ecology," or large-scale, multidisciplinary, highly collaborative, integrated research programs [*Coleman,* 2010].

The IBP's goal was to better understand the biological basis of productivity and human welfare, and it focused on major biomes using a holistic approach to both field research and modeling efforts [*Golley,* 1994]. One unintended consequence of the ecosystem approach, which may have been partially fueled by some of the associated personalities, was that the IBP alienated many organismal, population, and evolutionary ecologists [*Hagen,* 1992]. The fallout from this rift continues to be a challenge for the development of a more integrated ecological science to this day.

For NSF, the next step after the IBP was to envision, articulate, and initiate a more integrative program that built on the IBP-proven success of the ecosystems approach. One outcome, following several community-based workshops, was the LTER program [*Callahan,* 1984]. Although there was a strong focus on ecosystem processes at the outset, LTER research has gradually expanded to reduce the earlier disciplinary rift by addressing broader ecological theory and including important subdisciplines both within and beyond ecology [e.g., *Jones et al.,* 2012; *Robertson et al.,* 2012]. In the time since its founding in 1980, the LTER program has grown from a small group of disparate sites to a cohesive, interactive, and societally relevant network that now includes 25 sites (Figure 1).

LTER Science and the Example of Net Primary Production

The kinds of science conducted and theories tested within any given LTER site as well as across the program, along with the methods and approaches, continue to evolve. One of the most important changes to occur has been the coalescence of independent sites into a coherent, collaborative network, an advance that has been repeatedly encouraged by the decadal reviews of the LTER program that NSF commissions.

Specifically, analysis of *Johnson et al.* [2010] showed how the LTER Network has evolved from a loose federation of independent sites to a highly collaborative and densely connected network. The evolution of this collaboration has produced broader generality.

For example, understanding patterns and controls of net primary production (NPP) is one of the core research activities at all LTER sites. NPP is considered to be a fundamental variable that integrates many ecosystem processes [*McNaughton et al.,* 1989], and it is one of the major pathways in the carbon cycle. Therefore, understanding what controls NPP has a significant effect on how we deal with global change.

Before LTER, it was well established that NPP increases with increasing mean annual precipitation up to about 200 centimeters. At that point, NPP is limited more by sunlight than by precipitation. This also implies that wet ecosystems are less efficient at converting energy into NPP than drier ecosystems.

In one of the earliest efforts of cross-site synthesis, *Knapp and Smith* [2001] analyzed more than 10 years of NPP data from 11 LTER sites to determine which biomes (e.g., desert, grassland, or forest) were most sensitive to interannual variability in precipitation. Such empirical information is useful for understanding ecosystem vulnerability in a future that will likely include more extreme climate events. In this case, *Knapp and Smith* [2001] determined that interannual variability in NPP was highest in mesic grasslands, compared to forests or deserts. They also found that NPP increased more in wet years than it decreased in dry years, suggesting that NPP exhibits stability in years of lower than average precipitation (Figure 2).

Following up on these findings, *Huxman et al.* [2004] found that during very dry years, the efficiency by which energy is converted to NPP across ecosystems converged on a value characteristic of arid environments, where water stress is the norm. That is, all ecosystems converged on a similar ratio between NPP and annual precipitation, defined as rain use efficiency, under drought conditions.

From Data to Knowledge: NPP's Relationship With Species Diversity

Understanding patterns of temporal variability in net primary production clearly requires long-term data. It is also vital to identify the mechanisms that either enhance or reduce ecosystem variability over time. Ecological stability is essentially the opposite of variability, and stability can be considered a measure of ecosystem resistance to environmental change. Unstable or highly variable ecosystems may more easily cross tipping points and transition into alternative stable states [*Scheffer et al.,* 2012].

By S. L. Collins and D. L. Childers

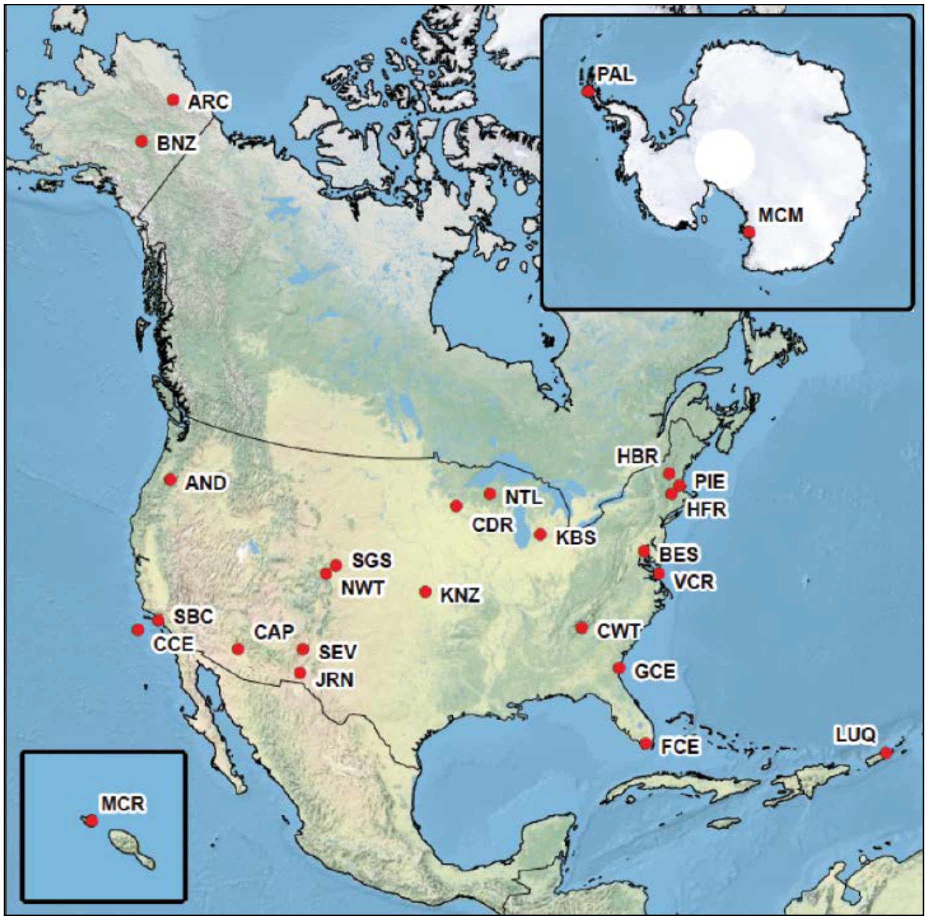

Fig. 1. A map showing locations of sites in the U.S. Long-Term Ecological Research (LTER) Network. Site codes are as follows: AND, Andrews Forest; ARC, Arctic/Toolik Lake; BES, Baltimore Ecosystem Study; BNZ, Bonanza Creek; CAP, Central Arizona–Phoenix; CCE, California Current Ecosystem; CDR, Cedar Creek; CWT, Coweeta Experimental Forest; FCE, Florida Coastal Everglades; GCE, Georgia Coastal Ecosystems; HBR, Hubbard Brook; HFR, Harvard Forest; JRN, Jornada; KBS, Kellogg Biological Station; KNZ, Konza Prairie; LUQ, Luquillo Forest; MCM, McMurdo Dry Valleys; MCR, Moorea Coral Reef; NTL, North Temperate Lakes; NWT, Niwot Ridge; PAL, Palmer Station; PIE, Plum Island Ecosystem; SBC, Santa Barbara Coastal; SEV, Sevilleta; VCR, Virginia Coast Reserve. Note that the Shortgrass Step site (SGS) is no longer in the network.

For example, *Hallett et al.* [2014] used LTER data from multiple grassland sites to show that mechanisms controlling temporal stability in grassland communities varied across the same precipitation gradient that drives NPP. These mechanisms ranged from high species diversity to high dominance by stabilizing species.

All of these syntheses used long-term data sets (NPP and plant community composition), often from the same sites, to address fundamental theory regarding stability and variability of NPP, a key ecosystem process; none of these studies would be possible without the collaborative approach promoted by networks such as LTER.

Strengths and Limitations of LTER

The LTER Network has many obvious strengths—including a long history of well-documented, long-term, observational, and experimental research—but it also has its limitations.

The location of sites is somewhat idiosyncratic because in most cases the network was expanded by funding the most competitive proposals and not with a focus on geographic distribution and representativeness. Second, research across the network does not necessarily address all drivers of global environmental change. Also, because the initial focus was on independent site-based research, the coordination and integration of heterogeneous long-term data to generate broader understanding remains a challenge.

As a consequence, the nature of collaboration within and beyond LTER continues to evolve. Recently, *Fraser et al.* [2013] called for the development of networks of coordinated, distributed experiments (CDEs) that should help eliminate or minimize some of the challenges inherent in attempts to synthesize existing but somewhat disparate data sets. CDEs are hypothesis-driven experiments that are replicated over multiple geographic locales and include a standard research design agreed upon by all participants. CDEs control for differences in spatial and temporal scales, are typically inexpensive to carry out at the site level, and may be implemented globally.

One example of a participant-driven CDE is the Nutrient Network (NutNet), a global network of more than 50 grassland sites [*Borer et al.*, 2014]. NutNet links together U.S. LTER, International LTER (ILTER), and many non-LTER sites in a coordinated experiment to determine the effect of nutrient limitation on the composition, structure, and diversity of grassland communities.

This CDE has produced high-impact results. For example, one fundamental theory in ecology is the "hump-backed" model of the species diversity-productivity relationship [*Grime*, 1973], which predicts that species diversity will be highest at intermediate levels of NPP. *Adler et al.* [2011] found little support for this widely cited theory. In a follow-up study, *Hautier et al.* [2014] quantified the effect of fertilization, a treatment that simulates nutrient enrichment, on the temporal stability of grassland NPP. They found that when the abundance of some species increased, that of others decreased, and there was little net change in total NPP.

Fertilization, however, reduced species diversity, leading to less compensation and lower ecosystem stability. Given that atmospheric nitrogen deposition is increasing globally, this important test of stability theory suggests that many ecosystems are highly vulnerable to this global environmental change.

LTER in the Context of Other Observatories

Other models for the organizational structure of networks may be found in several new emerging observatory networks, including those sponsored by NSF: the Ocean Observing System (OOS), Critical Zone Observatories (CZO), and the National Ecological Observatory Network (NEON). Examples of global networks include the Global Lakes Ecological Observatory Network (GLEON), FluxNet, the Center for Tropical Forest Science (CTFS), and ILTER. In particular, synoptic networks of research infrastructure, such as NEON and

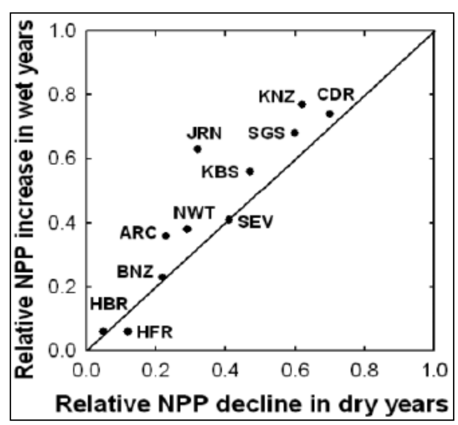

Fig. 2. Analysis of temporal variation in net primary production (NPP) at 11 LTER sites showing the relative decline in NPP during the driest year in the time series versus the relative increase in NPP during the wettest year in the time series. In general, NPP increases more in wet years than it declines in dry years. Site abbreviations are as in Figure 1. Modified from Knapp and Smith *[2001].*

EarthScope, are explicitly designed to collect ecological and environmental data using standardized, prescribed field methods and sensor arrays at continental scales.

To some extent, the development of these national and global networks reflects an understanding of the value of long-term, large-scale environmental data, as demonstrated by the success of the LTER Network. Moreover, the LTER Network and many other observatory networks are highly complementary: The infrastructure networks will generate long-term observational data across many biomes globally, while LTER and similar research networks (CZO, ILTER, and CTFS) will continue to provide a more detailed mechanistic understanding of environmental change.

Together, these networks have tremendous synergistic potential, but the biophysical research community faces a daunting challenge: to weave together these diverse research and monitoring networks into a fully integrated global environmental data-gathering platform. This integration is essential if scientists, decision makers, and society are to fully utilize and synthesize massive data streams in order to better understand and manage Earth's ecosystems and their responses to global environmental change.

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Author Information

Scott L. Collins, Department of Biology, University of New Mexico, Albuquerque; email: scollins@sevilleta.unm.edu; and Daniel L. Childers, School of Sustainability, Arizona State University, Tempe