

Long-Term Ecological Research in a Human-Dominated World

G. PHILIP ROBERTSON, SCOTT L. COLLINS, DAVID R. FOSTER, NICHOLAS BROKAW, HUGH W. DUCKLOW, TED L. GRAGSON, CORINNA GRIES, STEPHEN K. HAMILTON, A. DAVID McGUIRE, JOHN C. MOORE, EMILY H. STANLEY, ROBERT B. WAIDE, AND MARK W. WILLIAMS

The US Long Term Ecological Research (LTER) Network enters its fourth decade with a distinguished record of achievement in ecological science. The value of long-term observations and experiments has never been more important for testing ecological theory and for addressing today's most difficult environmental challenges. The network's potential for tackling emergent continent-scale questions such as cryosphere loss and landscape change is becoming increasingly apparent on the basis of a capacity to combine long-term observations and experimental results with new observatory-based measurements, to study socioecological systems, to advance the use of environmental cyberinfrastructure, to promote environmental science literacy, and to engage with decisionmakers in framing major directions for research. The long-term context of network science, from understanding the past to forecasting the future, provides a valuable perspective for helping to solve many of the crucial environmental problems facing society today.

Keywords: coupled natural–human systems, cyberinfrastructure, environmental observatories, environmental education, socioecological systems

The US Long Term Ecological Research (LTER) Network was started in 1980 to provide sites for ecologists to address questions that require long periods of study in order to be resolved. Hypothesis-driven research conducted over an extended period is a hallmark of the LTER Network today and the foundation of its scientific contributions (see Callahan 1984, Franklin et al. 1990, Hobbie et al. 2003). At 26 sites (figure 1), ecologists conduct synthetic and cross-site research that builds on site-based data, experiments, and models across diverse regions.

Historically, studies at LTER Network sites have addressed long-term questions not easily addressed in short-term funding cycles: How do populations change in response to long-term environmental forcings such as landscape and climate change? How do these changes affect biodiversity and trophic interactions and, in turn, primary productivity, element cycles, and other ecosystem processes? What are the lags in ecosystem responses to and the legacies of past human and natural disturbances? What precipitates ecological tipping points, and are such changes predictable?

These questions are broadly applicable to all ecosystems, and as the value of addressing them became clear during the first 20 years of the program, the LTER Network grew to include additional biomes and ecosystem types, to encompass broader regional scales of inquiry, and to incorporate

human-dominated systems in its research. Today's network of forest, grassland, desert, freshwater, coastal, and other ecosystems spans a broad geographic range of both climate and human impact. Climates within the network range from polar to tropical and from maritime to continental, with correspondingly diverse biotic assemblages. Human influences among sites range from no intentional disturbance to intensive management for agricultural, rangeland, forestry, and urban outcomes.

Creation of the network thus substantially altered the range of research sites used by US ecologists. Although sites in national parks, national forests, agricultural experiment stations, and biological field stations have historically provided a rich context for asking long-term ecological questions, most questions have been addressed in an ad hoc manner. The LTER Network provides an explicit opportunity to document ecological changes and to simultaneously address long-term questions across a broad array of ecosystems. Documenting these changes provides an important opportunity to ask mechanistic questions about the causes and consequences of change, an additional hallmark of LTER: place-based long-term experimentation (Knapp et al. 2012 [in this issue]).

The ability to link results at one site to findings at another allows the exploration of questions at broader geographic

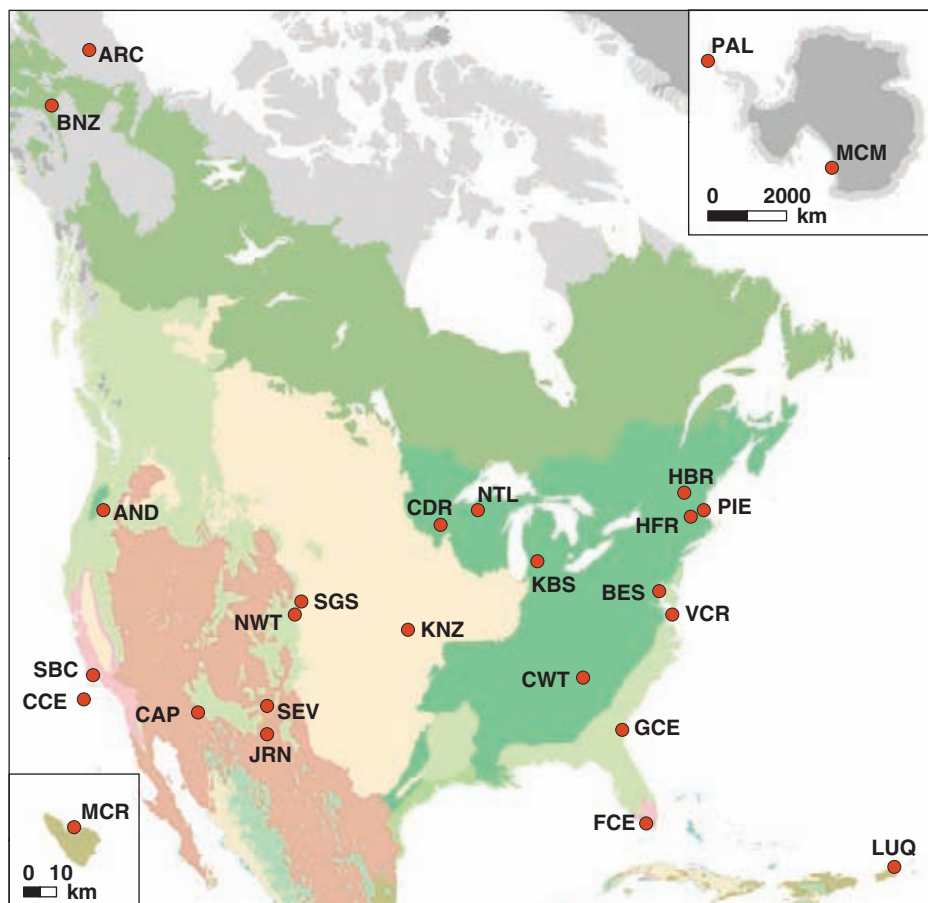


Figure 1. Map of the 26 Long Term Ecological Research Network sites on an ecoregion map from Olson and colleagues (2001). Descriptions of the sites can be found at www.lternet.edu. Abbreviation: km, kilometers. For the site-name abbreviations, see Knapp and colleagues' (2012) table 1 (in this issue, on p. 379).

scales in order to explore both regional patterns and controls, as well as to explore the degree of connectivity among disparate parts of regional and continental landscapes (*sensu* Peters et al. 2008). By the end of the network's third decade, the number of cross-site studies had ballooned (figure 2; Johnson et al. 2010). The following five examples demonstrate this development:

(1) In the Long-Term Intersite Decomposition Experiment, the decomposition rates of leaf litter and roots were measured in a 10-year reciprocal-transplant experiment among 21 long-term sites in seven biomes. The results showed that relatively simple models can predict decomposition rates on the basis of litter quality and regional climate (Gholz et al. 2000) but that the rate of nitrogen release from leaf litter is largely independent of climate (Parton et al. 2007). Nitrogen release instead depends on the initial tissue nitrogen concentrations and mass, except in arid environments in which exposure to large amounts of ultraviolet radiation overrides the influence of nitrogen content.

(2) In the Lotic Intersite Nitrogen Experiment (LINX), a set of comparative studies of nitrogen dynamics were conducted

in 70 headwater streams from across North America on the basis of collaborations that grew out of the LTER Network and later included other sites. Using coordinated whole-stream nitrogen-15 isotope-addition experiments, LINX studies demonstrated the importance of headwater streams for maintaining downstream water quality (Peterson et al. 2001, Helton et al. 2011), quantified their sensitivity to excess nitrate loading (Mulholland et al. 2008), and clarified their role as sources of the potent greenhouse gas nitrous oxide (Beaulieu et al. 2011). LINX research has now expanded to include nitrogen cycling in large rivers and wetlands in addition to streams.

(3) In a study of very long-term records of lake ice initiated at LTER Network sites and then expanded to other Northern Hemisphere locations, Magnuson and colleagues (2000) exposed a trend of shorter and more variable durations of ice cover over the past century. These trends of reduced ice cover offered an integrated, long-term indication of a warming climate over broad geographic regions.

(4) A working group convened at the National Center for Ecological Analysis and Synthesis to examine the relationship between plant productivity and diversity at LTER Network and other sites (Waide et al. 1999) led to a meta-analysis of over 170 studies of species richness and productivity (Mittelbach et al. 2001), which changed the prevailing view that species richness peaks at intermediate productivities. Building on this result, a more recent multi-site international experiment that included LTER Network sites showed that species richness per se cannot be used to predict productivity, except in reconstructed communities (Adler et al. 2011).

(5) An analysis of more than 900 species responses from 34 nitrogen-fertilization experiments across long-term sites (Cleland et al. 2008) showed that trait-neutral and trait-based mechanisms operated simultaneously to influence diversity loss as net primary production increased with fertilization (Suding et al. 2005). Although soil-buffering capacity modulated some responses (Clark et al. 2007), low abundance was consistently an important driver of species loss across ecosystems, and both trait-based and species-specific responses were also evident (Pennings et al.

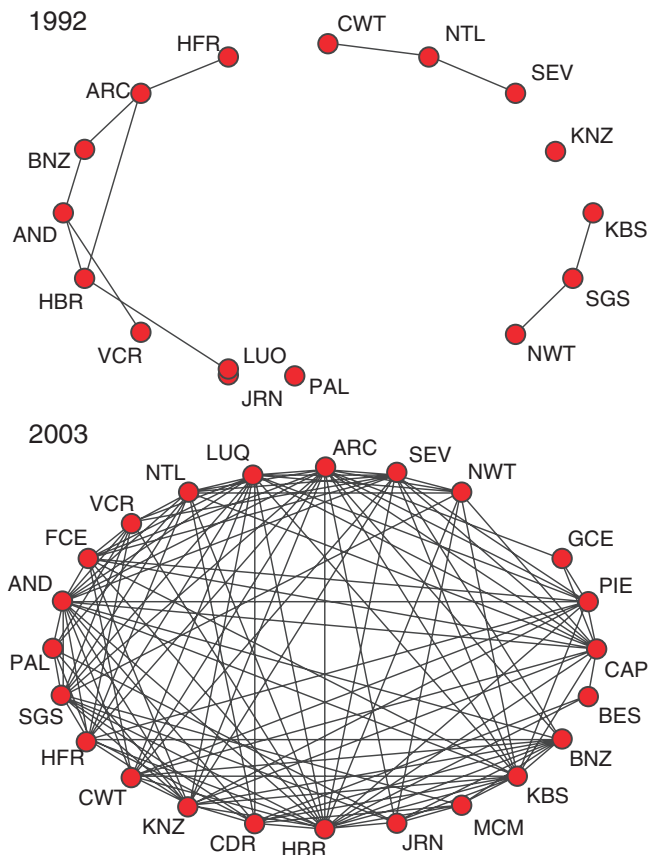


Figure 2. Evolution of cross-site research in the Long Term Ecological Research Network in the decade prior to 2003, quantified by joint intersite publications (lines between sites), recalculated from the data in Johnson and colleagues (2010). For the site-name abbreviations, see Knapp and colleagues' (2012) table 1 (in this issue, on p. 379).

2005, Cleland et al. 2011). The results from these syntheses demonstrated that rarity, species identity, functional traits, and physical environment all contributed to changes in plant-community composition in response to soil nitrogen availability.

Clearly, cross-site syntheses add substantial value to highly mechanistic site-based analyses and provide the opportunity to develop and test ecological theories that can lead to broader ecological knowledge.

The new emergence of environmental observatories—including the National Ecological Observatory Network (NEON; Keller et al. 2008); the Oceans Observatory Initiative (Isern and Clark 2003); the Global Lake Ecological Observatory Network (Kratz et al. 2006); and others, including open-source networks such as NutNet (Adler et al. 2011)—underscores a growing scientific appreciation for the power of cross-site observations (Carpenter 2008, Robertson 2008). The LTER Network was not designed to be a single integrated observatory in which each site employs standardized instrumentation and capacity,

as does NEON, nor are network sites optimally located to capture environmental trends at continental scales. Rather, the LTER Network was designed to provide key places for long-term, biome-specific observations and experimentation, where investigations can reveal the underlying causes and future consequences of patterns detected by distributed observatories that include LTER Network sites. And by increasingly engaging with diverse stakeholders—land managers, policymakers, and decisionmakers at all levels—LTER Network scientists can ensure that their inquiries are relevant to addressing societal concerns (Driscoll et al. 2012 [in this issue]).

LTER Network sites also play a unique role in science education at all levels. The sites are closely associated with institutions of higher learning, and graduate, undergraduate, and postdoctoral scholarship at these sites serves to advance ecology, as well as to introduce undergraduates to field research and graduate and postdoctoral scientists to the value of distributed research networks (e.g., Kane et al. 2008). Researchers at the sites are also actively engaged with local communities and with state and national agencies and boards, through which they can advance a range of informal education approaches, including professional advancement and environmental training for community leaders. The resulting synergies have included contributions to kindergarten through twelfth grade (K–12) science education through professional-development activities for science teachers (e.g., McKnight 2010), broadening and strengthening of local and state science curricula, and pedagogical contributions to the development of an environmental literacy movement, as is described below. These diverse educational efforts are increasingly providing new avenues for improving the quality and relevance of LTER science (Driscoll et al. 2012).

As the LTER Network enters its fourth decade, it is poised to contribute substantively to helping society respond to the ever-growing challenges of environmental sustainability, including climate-change mitigation and adaptation. How will the network help meet these challenges? In this article, we describe the vision of that future that emerged through a multiyear process of engagement across and beyond the entire LTER community, its National Science Foundation (NSF) associates, and colleagues from many other programs, observatories, and agencies.

We first lay out the place of LTER in a world increasingly subject to human influence. We describe a common framework for addressing important questions and examples of three overarching research themes that can best be addressed with a network of sites: landscape vulnerability and resilience to global change, cryosphere loss, and coastal-zone climate change. We then describe LTER contributions toward building environmental science literacy among K–12 students, undergraduates, and those who work with broader audiences, as well as the cyberinfrastructure demands of long-term ecological science and the network's approach to meeting these needs.

LTET in a human-dominated world

Thirty years of LTER Network research have yielded valuable knowledge about ecosystem change in response to both natural and human influences. Changes ranging from climate alteration to species introductions and to land- and water-use decisions have far-reaching impacts on ecosystem function, community structure, and population and evolutionary dynamics, which in turn strongly affect the critical ecosystem services on which we all depend. Ecological research seeks to test theory and to provide the empirical knowledge needed to forecast change and to devise effective management and policy responses. And theory and knowledge increasingly cross the boundary between natural and human systems, effectively linking science with policy (Liu et al. 2008, Driscoll et al. 2012).

A framework for exploring coupled natural–human systems over the long term. Several recent studies have shown how couplings between human and natural systems exhibit nonlinear dynamics across space, time, and organizational scales and have revealed complexities that cannot be disentangled by ecological or social research alone. The importance of understanding these dynamics cannot be underestimated: Without understanding the couplings between natural and human systems, workable policy solutions to some of the most recalcitrant environmental problems of today, which range from degraded water quality to biodiversity loss to climate-change vulnerability, will remain difficult to design and even more difficult to achieve.

At individual LTER sites, research on the couplings between natural and human systems has a rich history, ranging from inherently coupled working lands (row crop systems, timber plantations, grazing lands, coastal fisheries) to urban and exurban areas and sites in which direct human impact ceased decades ago but in which its legacies continue to condition ecosystem patterns and processes. In fact, no LTER Network site is uncoupled from human influence: The network's most remote Arctic and Antarctic sites are also affected by human decisions and behaviors, although humans are far away and their effects mostly unintentional. As a whole, the LTER Network provides a broad range of sites with differing intensities of human influence, degrees of intent, and levels of connectedness (Peters et al. 2008).

The integration of social and ecological research within the context of LTER Network sites and scientists (Redman et al. 2004), coupled with a rich ecological information base for the sites, is a promising new research frontier for LTER. The network has responded to this challenge by adopting as an organizing framework a common model that provides a standardized terminology and generalized structure to facilitate investigations of a wide variety of questions. The press–pulse dynamics (PPD) model (Collins et al. 2011) provides a comparative framework to integrate the biophysical and social sciences through an understanding of how human decisionmaking and behaviors interact with natural

processes to affect the structure, function, and dynamics of ecosystems and the services they provide to people.

The PPD model (see Collins et al. 2011, but cf. figure 3) is iterative, with linkages and feedbacks between biophysical and social domains (in figure 3, environmental and human systems, respectively). Model linkages are mediated by the biophysical system's delivery of ecosystem services and by the perception of these services by the social system. Model feedbacks are mediated by how services change human outcomes, perceptions, and behaviors that in turn affect the biophysical systems and their capacity to deliver subsequent services. Behavioral changes in the PPD model range from shifts in consumer preferences to environmental and energy policies and reproduction and migration rates. Such changes deliver to the biophysical system short-term pulses, such as nutrient inputs, fires, and management interventions, as well as long-term presses, such as atmospheric carbon dioxide loading, climate change, nitrogen deposition, and sea-level rise. In time, presses, pulses, and pulse–press interactions affect community structure and ecosystem function (Smith et al. 2009), eventually changing the delivery of ecosystem services such as the provision of food and fiber, pest and disease suppression, soil fertility, greenhouse gas stabilization, and clean water.

There are many potential socioecological questions that could be asked across a network of long-term sites. Building on a long history of prior research, LTER Network sites and scientists have identified several environmental challenges that represent critical issues for science and society that the network seems particularly well positioned to address today, including (a) landscape vulnerability and resilience to climate and land-use change, (b) the consequences of cryosphere loss and changes in associated services that range from urban water supply to rural livelihoods, and (c) coastal-zone climate change as it interacts with rising sea levels and coastal population change. For each of these

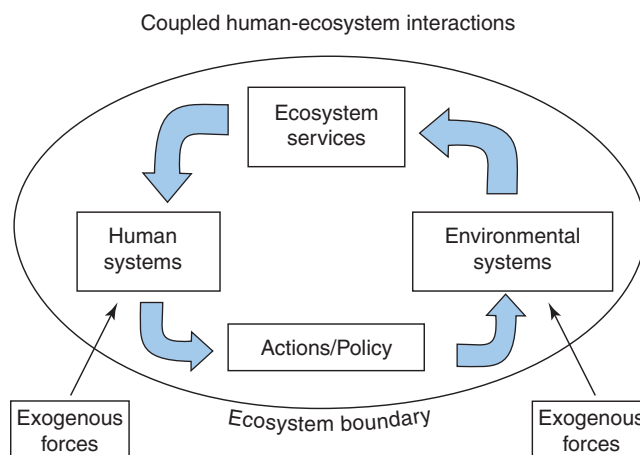


Figure 3. A press–pulse dynamics (PPD) framework, simplified for use by K–12 learners. The complete PPD model with more comprehensive linkages and feedbacks is available in Collins and colleagues (2011).

challenges, a comprehensive socioecological framework is required for them to be addressed effectively; each is best addressed with long-term observations and experiments in multiple locations; and for each, a subset of network sites in partnership with other networks and observatories could provide a core set of locations at which questions could be effectively addressed.

Future scenarios: Examining landscape vulnerability and resilience to global change. Science to help us understand, anticipate, and adapt to global change, including land-use and climate change, is becoming an ever more pressing need. How will global change alter the future of regional socioecological systems, and how and why do regional systems differ in vulnerability, resilience, and adaptability to change? These questions cannot be addressed by discipline-bound thinking but, rather, require new approaches that also incorporate broad-scale comparative investigations of diverse systems. One such approach is that of scenario studies (e.g., Baker et al. 2004, Thompson et al. 2012 [in this issue]), which provide a framework for addressing socioecological questions by crafting and evaluating suites of plausible scenarios that follow from current and historical trajectories. By examining multiple visions of the future that reflect a range of assumptions about land and water use, the burden of prediction is lifted, and comparisons among contrasting scenarios can be used to understand the dynamics of complex systems. New insights come from the examination of the perceived bounds of plausibility and from the discovery of commonalities across scenarios. Indeed, intrinsic vulnerabilities and robust management strategies are often identified when patterns recur across disparate scenarios.

Depictions of future scenarios are often articulated by regional stakeholders, including residents, policymakers, and social and ecological scientists, in order to illustrate major strategic choices (Hoag et al. 2005). These qualitative scenarios can be an end in themselves, or they may lead to quantitative simulations of future landscape change. This is frequently an iterative process whereby the narratives inform and are in turn informed by integrated spatial models of socioecological change that might include, for example, agent-based models that link land-use change, econometric, and ecosystem process models (Evans and Kelly 2004). At its best, fundamental site-based science underpins the development of the scenario-to-simulation framework, the creation of which is itself a form of scientific synthesis. This approach for coupling qualitative and quantitative scenarios has informed prescient planning and policy decisions and has generated a rich set of fundamental research questions.

For example, researchers at the Harvard Forest LTER site have begun a statewide scenario-studies project to examine the future of Massachusetts's forests. Their work began with a landscape-simulation study to examine the relative influence of 50 more years of the current trends in forest conversion, timber harvest, and climate change in terms of their effects

on forest carbon storage and tree species composition (Thompson et al. 2011). This work was rooted in 20 years of ecological research at Harvard Forest. Researchers then convened a group of around 12 stakeholders, including natural-resource managers and decisionmakers from state government, representatives from conservation nongovernmental organizations, and academics from multiple disciplines. They asked this group to chart three alternative futures of their choosing to compare with the current trends that had already been modeled. Through spirited discussion, the group settled on (a) a "free-market future," characterized by a rollback in environmental regulations and incentives for new business; (b) a "resource-limited future," characterized by high energy prices, a resurgence of agriculture, and a strong demand for woody-biomass energy; and (c) a "green-investment future," characterized by government incentives for conservation, green energy, and land-use planning. Through an iterative process with stakeholders, the researchers were able to describe the types, distribution, and intensity of land uses under each of the scenarios. Each of the scenarios is now being integrated into a simulation framework, which will superimpose the land-use scenarios onto a common template of climate-change and ecological dynamics. The goal is to examine the aggregate and interactive effects of land use within each scenario, as well as to make comparisons across the scenarios. Clearly, none of the scenarios will manifest exactly as they were described; nonetheless, by examining multiple potential pathways, the effort should reveal characteristics of the Massachusetts landscape that are particularly vulnerable or resilient to the interactive effects of land-use and climate change.

Cryosphere loss. The Earth's cryosphere, which includes sea, lake, and river ice; glaciers; seasonal snow; and ice-rich permafrost, harbors over 80% of the freshwater on the planet. The cryosphere cools the planet through its albedo; regulates the global sea level; stores substantial stocks of carbon; insulates soil from subfreezing air temperatures; and serves as a seasonally refreshed water supply for human consumption, irrigation, nutrient transport, and waste disposal. The prospect of accelerated cryosphere loss under a warming climate portends great ecological change and poses enormous threats to these ecosystem services, with attendant social and economic costs. A 1-meter sea-level rise, now thought to be unavoidable with a 600–1000 parts per million atmospheric carbon dioxide peak over the coming century (Solomon et al. 2009), alone represents an estimated economic impact of \$1 trillion that will be borne disproportionately by North America (Anthoff et al. 2010).

The extent and rates of cryosphere loss are increasingly well monitored, and our ability to project the future rates of cryosphere decline is improving. However, the ecological consequences—and especially the nature and extent of and economic impacts on human society and institutions—are still poorly understood. Cryosphere loss represents an inadvertent press event caused by human decisions—driven

by policies and markets—to extract energy from fossil fuel and to clear forests and other carbon-storing ecosystems for economic development. Changes in wintertime temperatures and snowfall will dramatically affect community structure and ecosystem processes in high-latitude and alpine ecosystems, but the effects will be felt even in arid, low-latitude ecosystems that depend on mountain meltwater for seasonal water supplies—riverine, floodplain, agricultural, and urban ecosystems in particular. Many of these effects will be social, since some of the most populous cities and productive farmland in North America depend on these water supplies.

Examples of cryosphere loss and its effects abound across the LTER Network, from Arctic sites undergoing long-term permafrost melt to Antarctic and northern lake sites losing ice cover and terrestrial sites experiencing shorter periods of snow cover and more-frequent freeze–thaw events. Alpine communities, such as that at the Niwot Ridge LTER site, illustrate the degree of subregional connectivity involved (figure 4): Hydrological connectivity is driven by the duration and timing of the seasonal snowpack and snowmelt, and under a warming climate, increasing windborne dust will accelerate snowpack and glacial melt, which will result in the snowline's moving to a higher elevation, which will in turn decrease hydrologic connectivity. With elevated nitrogen inputs from windborne dust and Denver air pollution, plant species diversity will decrease as alpine areas shrink, shrubland will expand, and the landscape will become more homogeneous. Exacerbating these trends is the regional outbreak of mountain pine beetles that will remove a large portion of the subalpine forest.

Cryosphere change and its consequences are played out as long-term trends that in many places will be difficult to discern from short-term variability in climate and other environmental factors and in social dynamics, such as population and economic change. Long-term sites provide the perspective necessary to detect trends that would otherwise not be visible against this variability. And networked sites provide the potential for comparative tests of hypotheses that link cryosphere loss, ecosystem services, and human decisions, using, for example, the PPD model (figure 3).

Key research questions (Fountain et al. 2012 [in this issue]) include (a) how climate regulation is affected by feedbacks from thawing permafrost and sea ice, especially because of the release of vast stores of carbon and changes in albedo, and what the implications are for regional and global economies and policies, including sovereignty; (b) what the economic implications of snow and ice loss are, including the future of winter recreation and related cultural activities; (c) how changing snowpack—the amount and timing of water storage and delivery—in the western United States will influence the economies of this region, and whether the impacts will be disproportionately imposed on disadvantaged groups; and (d) what the cultural mechanisms are by which cryosphere loss influences public opinion and what policies and legal instruments are most effective for

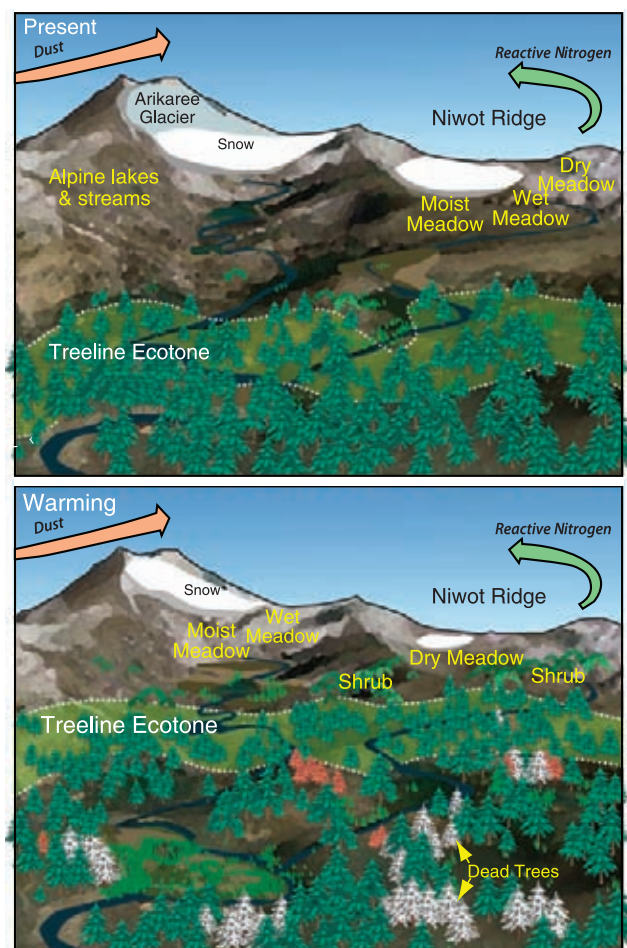


Figure 4. Expected changes in hydrologic connectivity related to cryosphere loss at the Niwot Ridge Long Term Ecological Research Network site. As windborne dust deposition increases in a warming climate, snowpack and glacial melt will be accelerated, which will result in a higher snowline, a shrunken alpine area, and the expansion of shrubland, exacerbated by a climate-induced mountain pine beetle outbreak that is now decimating the subalpine forest. This figure was created by Eric Parish.

environmental protection, impact mitigation, and adaptation in the face of climate change. The PPD model provides an effective means for linking cryosphere change with the ecosystem dynamics that lead to altered ecosystem services and then with subsequent human activities that may—through policies, behaviors, and markets—either slow or hasten cryosphere loss.

Coastal-zone climate change. Because they are at the interface of continental and oceanic realms, coastal systems are expected to be especially affected by climate change and to experience effects from both land and sea. With more than 50% of the US population living in coastal counties, many changes will play out in human communities and economies. Coastal-zone research sites, including nine

LTER Network and many additional partner sites, differ in their biophysical vulnerability to the coastal impacts of climate change. Some ecosystems along the US eastern seaboard will be more affected by sea-level rise and storm-surge severities, and others will be more affected by ocean acidification (e.g., coral reef communities in the south Pacific), the loss of sea ice (Antarctica), or changes in water temperature and freshwater inflows. Human vulnerabilities will also differ among regions, which arises from differences in coastal population density and demographic composition and from the location and resilience of the regions' built infrastructure, which ranges from cities to drilling platforms. All of these effects and vulnerabilities need to be considered in concert in order to provide a comprehensive understanding of coastal-zone climate change and the potentials for future adaptation.

The need to understand and anticipate the effects of climate change, assess the vulnerabilities of natural and human elements of coastal systems, and adapt to or mitigate the effects of changes is prompting new efforts for integration across academic disciplines and creation of partnerships among academic, public, and governmental constituents. As for cryosphere loss, long-term studies are needed in order to document patterns and consequences of coastal-zone change. Unlike cryosphere loss, however, coastal-zone change is likely to be strongly episodic in response to storm events that are projected to be increasingly severe and whose inland consequences will, in any case, be magnified because of sea-level rise. Posing questions relevant to networked sites in the context of a common model allows for a fundamental understanding more difficult to gain from shorter-term or more geographically discrete research.

Key questions include (a) how the presses and pulses associated with coastal climate change—altered water temperature, precipitation, runoff, sea level, solar radiation, wind and wave climates, pH, and salinity—affect the structure and function of coastal ecosystems and what attributes affect the vulnerability of those ecosystems; (b) how climate-induced changes in coastal systems affect critical ecosystem services such as carbon sequestration, wildlife habitat, food-web support, and storm protection; (c) what attributes of human systems such as built infrastructure; land use; governance structures; and population demographics, including wealth and ethnicity, interact to influence human vulnerabilities to coastal climate change and how these interact with changes in ecosystem services to prompt responses of adaptation and mitigation; and (d) how mitigation and adaptation strategies, such as coastal engineering and reductions in greenhouse gases, would feed back to affect climate drivers and the structure and function of coastal systems. Effectively addressing these questions requires an approach that acknowledges and deeply explores the linked socioecological processes that underlie the delivery of almost all of the ecosystem services provided by coastal-zone environments.

Many LTER Network sites are located in coastal zones at different latitudes along the eastern and western US

seaboards, as well as in the South Pacific and Antarctic Oceans, and provide a diversity of geomorphologies and degrees of human influence, ranging from urban to exurban, rural, and natural. They are therefore well positioned to address a subset of these key questions, most of which will require a combination of long-term baseline data and experiments designed to predict the consequences of sea-level rise for the ecology of coastal communities.

Toward an environmentally literate populace

Society's ability to understand and act on the coupled natural and human systems on which we depend, built on a foundation of complex scientific inquiry, is key to a sustainable future. And it is the public—decisionmakers at all levels, from landowners and local officials to national leaders—who must act. The importance of an environmentally literate public is hard to overstate: From the grocery store and car dealership to the voting booth and corporate boardroom, individuals make choices that have far-reaching, collective consequences. Education helps to ensure that those choices are based at least in part on evidence and reasoning underpinned by solid scientific research.

The LTER approach to research, combined with an ability to implement long-term educational initiatives, has allowed for unique approaches to the training of future researchers and to the conveyance of ecological concepts and insights to a broad constituency. At individual network sites, educational activities range from K–12 students and teachers engaged in schoolyard ecology to undergraduates involved in field classes and research internships and to graduate students and postdoctoral scholars learning to frame questions and to conduct research in long-term and sometimes cross-site contexts. Public outreach in many forms reaches working professionals, as well as the general public, often through the education of those best positioned to communicate with the general public. This outreach is increasingly placed in a socioecological context, which illustrates the natural–human system couplings that are central to addressing major environmental issues and that are often hidden to many.

The vision for education in the LTER Network includes leveraging both long-term and cross-site perspectives to advance fundamental science learning by K–12, undergraduate, and graduate students and developing programs for key constituent and underrepresented groups. These groups include K–12 teachers, university students, education policymakers, and the professional public, which includes policymakers, natural-resource managers, the working media, and others whose success depends on access to and imparting of sound ecological knowledge.

A long-term framework for environmental science literacy. Environmental science literacy—the capacity to participate in and make decisions through evidence-based discussions of socioecological systems—is essential not only for many science careers but also for responsible citizenship.

Environmental science literacy requires citizens to understand, evaluate, and respond to multiple sources of information. The development of an environmental science literacy framework is crucial for providing this capacity among K–12 students, a key constituency that represents both future STEM (science, technology, engineering, and mathematics) professionals and the 75% of the US population that will not earn a higher degree. It is also important for framing information provided to university students, STEM professionals and the general public.

The development of an environmental literacy framework requires that we understand stakeholders' current state of knowledge in core areas and how math and science concepts are best used to provide a desired level of literacy. In this context, stakeholders range from K–12 students to the voting public. We know, in general, that for most stakeholders, the state of knowledge is low, which is reflected both in standardized K–12 test scores (Gonzales et al. 2008) and in college-level assessments of ecological concepts (e.g., Hartley et al. 2011). We also know that there are troubling demographic disparities and, in particular, persistent gaps in science and mathematics achievement between white students and students of color (Vanneman et al. 2009). Building a capacity for principle-based environmental reasoning in all stakeholders and broadening the participation of underrepresented groups in environmental science careers should be important components of all science education efforts (George et al. 2001, ESA 2006).

In K–12 education, the term *learning progressions* describes increasingly sophisticated ways of reasoning about an area of study, typically organized around a set of core topics that can be used to organize an integrated understanding of larger, complex issues (Duschl et al. 2007). A current effort within the network to build learning progressions into the K–12 science curriculum is being tested in 22 school districts across the country with an LTER Network-associated NSF Math and Science Partnership (MSP) award. In districts around four network sites, MSP participants—scientists and science educators working with a diverse mix of K–12 science teachers and students—are developing learning progressions around key science strands. These strands include carbon, water, and biodiversity, plus a mathematical strand that addresses quantitative reasoning and the mathematics of modeling and a citizenship strand focused on the roles of culture and place. All of these strands are deeply embedded in state science and mathematics standards and are connected by the theme of education for citizenship: how students take on roles as consumers and voters using evidence-based reasoning about personal decisions that have environmental consequences. Multidisciplinary themes focused on the human impacts of land-use, ecosystem structure, and ecosystem services offer rich experiences in STEM education that include atmospheric science, soil science, geology, agronomy, ecology, hydrology, computer science, and systems modeling. Placing these strands in a simplified PPD model (figure 3) provides an easily

understood context for showing coupled human–ecosystem interactions.

Two observations have emerged thus far from our LTER-based studies of learning progression. First, the PDD model embraced by the LTER Network (Collins et al. 2011) emphasizes that socioecological systems are organized as dynamic hierarchical systems. This basic tenet defines specific ways in which subjects or entities of interest are organized and interact with one another. Embedded in the concept is the notion of *scale*, wherein the boundaries between levels of interaction are defined by differences in the geographies and rates at which entities interact. Second, socioecological processes may include multiple principles that operate simultaneously in the social and ecological realms.

Our research in student learning and understanding of ecological systems indicates that students and teachers fail to adopt hierarchical reasoning when questioned about ecological systems and principles. The conservation of matter and energy is not understood. Processes operating at one scale are assumed to operate at the same scope and magnitude at other scales. The nature of the interconnectedness of systems is overstated (e.g., removal of one species leads to system collapse). Human social hierarchies and human agency are conflated with ecological hierarchies and processes and are applied to natural systems.

LTER Network research on learning progressions provides insights into how to advance student understanding of socioecological systems and also provides the scaffolding of science and social-science principles that is needed for students' environmental literacy—a key to understanding human agency and its application to the scale of action that the challenges demand and to engaging the broader public.

Engaging the broader public. Extending this understanding to older stakeholders—both the voting public in general and working STEM professionals, such as land managers, policy analysts, and public- and private-sector decisionmakers—presents a different set of challenges (Driscoll et al. 2012). Recent calls for a renewed effort by ecologists to engage in public outreach (e.g., Groffman et al. 2010) have noted that effective communication outside the classroom is influenced by learners' interests, prior knowledge, social networks, and values and beliefs. This requires issues to be framed in ways that resonate with the public and messages to be delivered in ways that acknowledge the importance of emerging forms of media and informal learning environments (NRC 2009). Effective communication can also involve partnerships with boundary organizations that specialize in fostering the use of science knowledge in environmental policymaking and management (Osmond et al. 2010). These organizations range from university-based extension programs at land-grant universities to individual site-based efforts.

One such site-based effort is the Science Links program at the Hubbard Brook LTER site. The program is explicitly aimed at communicating basic science findings at Hubbard

Brook to interested audiences that range from the general public to congressional staffers and is a particularly apt example of a way to leverage limited funding to broaden the impact of ecological findings. Outreach is initiated early in a project and is informed by a group of policy and natural resource management advisors who help to craft a message that is most relevant to the audience at hand. Such efforts can help to shorten an otherwise distressing lag between recognizing and addressing important environmental problems, such as those associated with acid rain (Likens 2010), as well as to help an increasingly dubious public to gain confidence in their ability to understand—and ultimately act on—complex environmental issues. More broadly, efforts to shape the public's perception of natural areas and to increase awareness of the linkages between human and natural systems (e.g., Foster 1999) are equally vital, and both targeted and more-generalized efforts to build public environmental literacy are important priorities for LTER.

Information for the future

Cyberinfrastructure describes the network of computing environments that support advanced data acquisition, storage, management, integration, mining, visualization, and other information-processing services (Atkins et al. 2003). When used for scientific purposes, cyberinfrastructure is a technical solution to the problem of efficiently connecting data, computers, and people.

The development of cyberinfrastructure is integral to the success of all environmental networks, including the LTER Network: Data for modeling and forecasting are essential for identifying the effects of accelerated and abrupt changes, and the explosion of real-time data availability calls for near-real-time analysis and distribution if those data are to be their most useful (AC-ERE 2009). Equally compelling is the need for data repositories and archives that allow the detection and synthesis of long-term trends and the effective integration of data from different networks and researchers.

That less than 1% of ecological data is accessible after the publication of derived results (Reichman et al. 2011) reveals the social and technological challenges of curating that environmental data. Data dispersion, heterogeneity, and provenance (Jones MB et al. 2006), coupled with cultural norms that provide few rewards, make ecological information systems difficult to design, implement, and incentivize. Nevertheless, fueled by the emergence of environmental observatories charged with collecting and making openly available data from a variety of sensors (e.g., NRC 2004) and by the success of efforts to assemble and synthesize networked data toward broader-scale tests of ecological theory (e.g., Mittelbach et al. 2001, Suding et al. 2005), new efforts to develop centralized ecological information systems are under way. The LTER Network, with its 30 years of experience in environmental information management, has been a pioneer in these efforts—a microcosm of the hard challenges and substantive benefits of networked ecological

data—and will be among those linked by centralized efforts such as DataONE (Michener et al. 2011).

The distributed data repositories of the 26 network sites reflect the vast diversity of ecological data and the breadth of approaches to environmental data-management systems as developed by field stations, museums, academic institutions, state and local governments, and individual scientists. Core LTER Network data conform to consistent metadata standards (Michener 2006) and are held by individual sites within Web-accessible catalogs. These data repositories, plus a network-wide policy of open data access, make data available to those wishing to assemble cross-site syntheses. Although open access has been crucial to the success of cross-site studies such as those noted earlier (e.g., Mittelbach et al. 2001, Parton et al. 2007), the structure of site data often differs from catalog to catalog, which makes the discovery and subsequent integration of semantically similar data a task that is, at best, inconvenient. What is needed is a central repository that maintains the veracity and provenance of site data but allows single-portal access.

Early examples include the climate and hydrology portals for LTER data. Centralized access to data from 26 sites provides an ability to detect and synthesize patterns and trends without the pain of querying 26 separate data catalogs with different keyword vocabularies and reporting units. Lowered transaction costs makes synthesis practical—and, in some cases, possible—when it had not been so previously, providing in this case a capacity to integrate multiple climate- and hydrologic-system components across disparate ecosystems and biomes to provide novel insights (Jones JA et al. 2012 [in this issue]). What we need next is an ability to perform these syntheses for all system components. The LTER Network Information System (NIS) is being developed to address this need.

The LTER NIS will provide access to data from the 26 network sites through a single point of access and at the same time ensure the long-term preservation of site data through centralized stewardship. Site data will continue to be curated at individual sites but will also be exposed to harvest by the NIS on a frequent, periodic basis. Further data processing will then provide common formats that can be easily queried by cross-network portals, such as EcoTrends (Peters et al. 2011), that are designed to create derived long-term data products and by storage systems such as DataONE that will provide a centralized facility for storing data from multiple sources, including the NIS. Importantly, the system will be scalable: Adding data from additional sites, whether they are existing field stations, sensor networks, future LTER sites, or individual field projects, will be straightforward.

The nature of LTER data—and by extension, ecological data in general—makes a single rigid method for storing and accessing them impractical. By design, many long-term data sets are collected using common protocols at regular intervals from specified locations. As priorities, resources, and technologies shift, however, intervals change, protocols

are improved, and locations sometimes become inappropriate or insufficient. Robust sampling programs will have precautions and methods in place to protect the veracity of long-term observations, including a data-management system sufficiently nimble to allow these changes. An additional challenge in ecological science, however, is archiving and exposing experimental data—data that may be collected over a short term, with additional protocols and different experimental treatments in a sampling matrix that may not correspond much with that of the long-term collection. This adds an additional important burden on information systems that aspire to address ecological science needs but also provides an invaluable opportunity for future users to query the full suite of observations available for a particular site or region.

Informal users also need to be accommodated. The best information system will make derived products available to a variety of potential users—not just scientists but also educators, students, decisionmakers, and the public. So long as data within the system are fully exposed to all portal developers, this accommodation will be straightforward, as might be the accommodation of data from nontraditional, more-uncertain sources, such as citizen science networks (Cohn 2008).

Conclusions

The US LTER Network enters its fourth decade with a sound record of scientific achievement in the ecological sciences. At each of the network's 26 sites, we have learned an extraordinary amount about the organisms and processes important at the biome it represents, about the way the site's ecosystems respond to disturbance, and about human influences and long-term environmental change. Cross-site observations and experiments are increasingly revealing how key processes, organisms, and ecological attributes are organized and behave across major environmental gradients. In total, research in the LTER portfolio is contributing substantially to our basic knowledge of ecological interactions and to our ability to forecast change and test ecological theory.

Against this backdrop, the LTER Network is undertaking a new kind of transdisciplinary science—one that ranges from local to global in scope, that blends ecological and social science theories, methods, and interpretations in order to better understand and forecast environmental change in an era when no ecosystem on Earth is free from human influence. Furthermore, the network is increasingly focused on conveying those results to an engaged audience of decisionmakers that can apply it. The LTER Network's PPD model provides a unifying framework for better understanding coupled natural-human systems across regions and temporal scales and a means for examining feedbacks and testing hypotheses about, first, how humans perceive the critical services provided by ecosystems; second, how these perceptions change behaviors and institutions; and third, how these changes in turn feed back to affect ecosystem structure

and function and the ability of these systems to indefinitely sustain their delivery of services.

Environmental literacy is an important ongoing legacy of LTER Network science and will remain so. Learners at all levels have benefited from LTER Network involvement: graduate and undergraduate students, K–12 students and educators, working professionals involved in land and resource management, policymakers, and the general public. Future efforts will be directed toward ensuring that these groups understand the linkages and feedbacks between social and ecological systems to better inform their ability to make evidence-based environmental decisions at all levels.

Advances in cyberinfrastructure are required in order to manage and organize the rapidly growing volume of ecological information and in order to enable integration and synthesis of that information over time. The LTER Network has led the ecological community in developing protocols and practices for documenting, curating, and sharing data, and it is now building the NIS, which will collect and curate data from LTER Network and other sites for storage in formats that can be queried by applications built to provide users with derived long-term data. Data in the system will thus be available to scientists, educators, students, decisionmakers, and the public for research, decision support, teaching, and informal education opportunities.

The LTER Network's primary mission is to use long-term observations and experiments to generate and test ecological theory at local to regional scales. Progress in solving environmental problems that today seem intractable depends on fundamental, long-term, integrated research that will generate a synthetic understanding of highly dynamic socio-ecological systems. Likewise, the early discovery of tomorrow's surprises depends on long-term research that provides a capacity to detect new trends. Extending these capacities to continental scales will provide the necessary experimental context within which to address the causes and consequences of change documented both by the LTER Network and by the emerging constellation of environmental observatories.

Acknowledgments

The LTER Network owes its success to the several thousand scientists who have used its sites and data to conduct groundbreaking ecological research and to the support and leadership provided by the National Science Foundation and state and federal agency partners. The network's principal partners include the US Forest Service, the Agricultural Research Service of the US Department of Agriculture, the US Fish and Wildlife Service's Bureau of Land Management, and the US Geological Survey. We thank three anonymous reviewers for insightful comments on an earlier version of this article.

References cited

[AC-ERE] US National Science Foundation Advisory Committee for Environmental Research and Education. 2009. Transitions and Tipping

- Points in Complex Environmental Systems. US National Science Foundation.
- Adler PB, et al. 2011. Productivity is a poor predictor of plant species richness. *Science* 333: 1750–1753.
- Anthoff D, Nicholls RJ, Tol RSJ. 2010. The economic impact of substantial sea-level rise. *Mitigation and Adaptation Strategies for Global Change* 15: 321–335.
- Atkins DE, Droegemeier KK, Feldman SI, Garcia-Molina H, Klein ML, Messerschmitt DG, Messina P, Ostriker JP, Wright MH. 2003. Revolutionizing Science and Engineering through Cyberinfrastructure. National Science Foundation. Report no. cise051203.
- Baker JP, Hulse DW, Gregory SV, White D, Van Sickle J, Berger PA, Dole D, Schumaker NH. 2004. Alternative futures for the Willamette River basin, Oregon. *Ecological Applications* 14: 313–324.
- Beaulieu JJ, et al. 2011. Nitrous oxide emission from denitrification in stream and river networks. *Proceedings of the National Academy of Sciences* 108: 214–219.
- Callahan JT. 1984. Long-term ecological research. *BioScience* 34: 363–367.
- Carpenter SR. 2008. Emergence of ecological networks. *Frontiers in Ecology and the Environment* 6: 228.
- Clark CM, Cleland EE, Collins SL, Fargione JE, Gough L, Gross KL, Pennings SC, Suding KN, Grace JB. 2007. Environmental and plant community determinants of species loss following nitrogen enrichment. *Ecology Letters* 10: 596–607.
- Cleland EE, et al. 2008. Species responses to nitrogen fertilization in herbaceous plant communities, and associated species traits. *Ecology* 89: 1175.
- Cleland EE, Clark CM, Collings SL, Fargione JE, Gough L, Gross KL, Pennings SC, Suding KN. 2011. Natural patterns of invasion in herbaceous plant communities are related to soil nitrogen and the functional similarity of native species. *Journal of Ecology* 99: 1327–1338.
- Cohn JP. 2008. Citizen science: Can volunteers do real research? *BioScience* 58: 192–197.
- Collins SL, et al. 2011. An integrated conceptual framework for social–ecological research. *Frontiers in Ecology and the Environment* 9: 351–357.
- Driscoll CT, Lambert KF, Chapin FS III, Nowak DJ, Spies TA, Swanson FJ, Kittredge DB Jr, Hart CM. 2012. Science and society: The role of long-term studies in environmental stewardship. *BioScience* 62: 354–366.
- Duschl RA, Schweingruber HA, Shouse AW, eds. 2007. *Taking Science to School: Learning and Teaching Science in Grades K–8*. National Academies Press.
- [ESA] Ecological Society of America. 2006. *Women and Minorities in Ecology II (WAMIE II): Committee Report, March 2006*. ESA.
- Evans TP, Kelley H. 2004. Multi-scale analysis of a household level agent-based model of landcover change. *Journal of Environmental Management* 72: 57–72.
- Foster DR. 1999. *Thoreau's Country: Journey through a Transformed Landscape*. Harvard University Press.
- Fountain AG, Campbell JL, Schuur EAG, Stammerjohn SE, Williams MW, Ducklow HW. 2012. The disappearing cryosphere: Impacts and ecosystem responses to rapid cryosphere loss. *BioScience* 62: 405–415.
- Franklin JF, Bledsoe CS, Callahan JT. 1990. Contributions of the Long-Term Ecological Research Program. *BioScience* 40: 509–523.
- George YS, Neale DS, Van Horne V, Malcom SM. 2001. In Pursuit of a Diverse Science, Technology, Engineering, and Mathematics Workforce: Recommended Research Priorities to Enhance Participation by Underrepresented Minorities. American Association for the Advancement of Science.
- Gholz HL, Wedin DA, Smitherman SM, Harmon M, Parton WJ. 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: Toward a global model of decomposition. *Global Change Biology* 6: 751–766.
- Gonzales P, Williams T, Jocelyn L, Roey S, Kastberg D, Brenwald S. 2008. Highlights from TIMSS 2007: Mathematics and Science Achievement of U.S. Fourth- and Eighth-Grade Students in an International Context. National Center for Education Statistics, US Department of Education. Report no. NCES 2009-001 Revised.
- Groffman PM, Stylinski C, Nisbet MC, Duarte CM, Jordan R, Burgin A, Previtali MA, Coloso J. 2010. Restarting the conversation: Challenges at the interface between ecology and society. *Frontiers in Ecology and the Environment* 8: 284–291.
- Hartley LM, Wilke BJ, Schramm JW, D'Avanzo C, Anderson CW. 2011. College students' understanding of the carbon cycle: Contrasting principle-based and informal reasoning. *BioScience* 61: 65–75.
- Helton AM, et al. 2011. Thinking outside the channel: Modeling nitrogen cycling in networked river ecosystems. *Frontiers in Ecology and the Environment* 9: 229–238.
- Hoag DL, Keske-Handley C, Ascough II J, Koontz L. 2005. Decision making with environmental indices. Pages 159–182 in Burk AR, ed. *New Trends in Ecology Research*. Nova Science.
- Hobbie JE, Carpenter SR, Grimm NB, Gosz JR, Seastedt TR. 2003. The US Long Term Ecological Research Program. *BioScience* 53: 21–32.
- Isern AR, Clark HL. 2003. The ocean observatories initiative: A continued presence for interactive ocean research. *Marine Technology Society Journal* 37: 26–41.
- Johnson JC, Christian RR, Brunt JW, Hickman CR, Waide RB. 2010. Evolution of collaboration within the US Long Term Ecological Research Network. *BioScience* 60: 931–940.
- Jones JA, et al. 2012. Ecosystem processes and human influences regulate streamflow response to climate change at long-term ecological research sites. *BioScience* 62: 390–404.
- Jones MB, Schildhauer MP, Reichman OJ, Bowers S. 2006. The new bioinformatics: Integrating ecological data from the gene to the biosphere. *Annual Review of Ecology, Evolution, and Systematics* 37: 519–544.
- Kane ES, et al. 2008. Precipitation control over inorganic nitrogen import–export budgets across watersheds: A synthesis of long-term ecological research. *Ecology* 89: 105–117.
- Keller M, Schimel DS, Hargrove WW, Hoffman FM. 2008. A continental strategy for the National Ecological Observatory Network. *Frontiers in Ecology and the Environment* 6: 282–284.
- Knapp AK, et al. 2012. Past, present, and future roles of long-term experiments in the LTER network. *BioScience* 62: 377–389.
- Kratz TK, et al. 2006. Toward a global lake ecological observatory network. *Publications of the Karelian Institute* 145: 51–63.
- Likens GE. 2010. The role of science in decision making: Does evidence-based science drive environmental policy? *Frontiers in Ecology and the Environment* 8: e1–e9.
- Liu J, et al. 2008. Complexity of coupled human and natural systems. *Science* 317: 1513–1516.
- Magnuson JJ, et al. 2000. Historical trends in lake and river ice cover in the Northern Hemisphere. *Science* 289: 1743–1746.
- McKnight DM. 2010. Overcoming “ecophobia”: Fostering environmental empathy through narrative in children's science literature. *Frontiers in Ecology and the Environment* 8: e10–e15.
- Michener WK. 2006. Meta-information concepts for ecological data management. *Ecological Informatics* 1: 3–7.
- Michener WK, et al. 2011. DataONE: Data Observation Network for Earth—Preserving data and enabling innovation in the biological and environmental sciences. *D-Lib Magazine* 2011, 17: 1–9. (17 January 2012; www.dlib.org/dlib/january11/michener/01michener.html)
- Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82: 2381–2396.
- Mulholland PJ, et al. 2008. Stream denitrification across biomes and its response to anthropogenic nitrate loading. *Nature* 452: 202–205.
- [NRC] National Research Council. 2004. *NEON: Addressing the Nation's Environmental Challenges*. National Academies Press.
- . 2009. *Learning science in informal environments: People, places, and pursuits*. National Academies Press.
- Olson DM, et al. 2001. *Terrestrial ecoregions of the world: A new map of life on earth*. *BioScience* 51: 933–938.

- Osmond DL, et al. 2010. The role of interface organizations in science communication and understanding. *Frontiers in Ecology and the Environment* 8: 306–313.
- Parton W, et al. 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science* 315: 361–364.
- Pennings SC, Clark CM, Cleland EE, Collins SL, Gough L, Gross KL, Milchunas DG, Suding KM. 2005. Do individual plant species show predictable responses to nitrogen addition across multiple experiments? *Oikos* 110: 547–555.
- Peters DPC, Groffman PM, Nadelhoffer KJ, Grimm NB, Coffins SL, Michener WK, Huston MA. 2008. Living in an increasingly connected world: A framework for continental-scale environmental science. *Frontiers in Ecology and the Environment* 6: 229–237.
- Peters DPC, et al. 2011. Long-term Trends in Ecological Systems: A Basis for Understanding Responses to Global Change. US Department of Agriculture, Agricultural Research Service.
- Peterson BJ, et al. 2001. Control of nitrogen export from watersheds by headwater streams. *Science* 292: 86–90.
- Redman CL, Grove JM, Kuby LH. 2004. Integrating social science into the Long Term Ecological Research (LTER) Network: Social dimensions of ecological change and ecological dimensions of social change. *Ecosystems* 7: 161–171.
- Reichman OJ, Jones MB, Schildhauer MP. 2011. Challenges and opportunities of open data in ecology. *Science* 331: 703–705.
- Robertson GP. 2008. Long-term ecological research: Re-inventing network science. *Frontiers in Ecology and the Environment* 6: 281.
- Smith MD, Knapp AK, Collins SL. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology* 90: 3279–3289.
- Solomon S, Plattner G-K, Knutti R, Friedlingstein P. 2009. Irreversible climate change due to carbon dioxide emissions. *Proceedings of the National Academy of Sciences* 106: 1704–1709.
- Suding KN, Collins SL, Gough L, Clark C, Cleland EE, Gross KL, Milchunas DG, Pennings S. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences* 102: 4387–4392.
- Thompson JR, Foster DR, Scheller R, Kittredge D. 2011 The influence of land use and climate change on forest biomass and composition in Massachusetts, USA. *Ecological Applications* 21: 2425–2444.
- Thompson JR, Wiek A, Swanson FJ, Carpenter SR, Fresco N, Hollingsworth T, Spies TA, Foster DR. 2012. Scenario studies as a synthetic and integrative research activity for long-term ecological research. *BioScience* 62: 367–376.
- Vanneman A, Hamilton L, Anderson JB. 2009. Achievement Gaps: How Black and White Students in Public Schools Perform in Mathematics and Reading on the National Assessment of Educational Progress. National Center for Education Statistics, US Department of Education. Report no. NCES 2009-455.
- Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, Dodson GI, Juday GP, Parmenter R. 1999. The relationship between primary productivity and species richness. *Annual Review of Ecology and Systematics* 30: 257–300.

G. Philip Robertson (robertson@kbs.msu.edu) is a professor with the W. K. Kellogg Biological Station and with the Department of Crop and Soil Sciences at Michigan State University, in Hickory Corners. Scott L. Collins is a professor in the Department of Biology at the University of New Mexico, in Albuquerque. David R. Foster is a professor in the Department of Organismic and Evolutionary Biology at Harvard University and director of the Harvard Forest in Petersham, Massachusetts. Nicholas Brokaw is a professor with the Institute for Tropical Ecosystem Studies at the University of Puerto Rico, in San Juan. Hugh W. Ducklow is a senior scientist and director of The Ecosystems Center at the Marine Biological Laboratory in Woods Hole, Massachusetts. Ted L. Gragson is a professor and chair of the Department of Anthropology at the University of Georgia, in Athens. Corinna Gries is a research scientist at the Center for Limnology at the University of Wisconsin, in Madison. Stephen K. Hamilton is a professor in the Department of Zoology and the W. K. Kellogg Biological Station of Michigan State University, in Hickory Corners. A. David McGuire is a professor in the Department of Biology and Wildlife at the University of Alaska, in Fairbanks, and is affiliated with the US Geological Survey. John C. Moore is a professor and director of the Natural Resource Ecology Laboratory at Colorado State University, in Fort Collins. Emily H. Stanley is a professor with the Center for Limnology at the University of Wisconsin, Madison. Robert B. Waide is professor of biology at the University of New Mexico, in Albuquerque, and executive director of the Long Term Ecological Research Network. Mark W. Williams is a professor in the Department of Geography at the University of Colorado, in Boulder.