Long-Term Ecological Research in a Human-Dominated World


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
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 multisite 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.

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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).
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.

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).
LTER 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 non-linear 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).](image-url)
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 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...
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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 socioecological 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.

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Science and Society: The Role of Long-Term Studies in Environmental Stewardship

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Long-term research should play a crucial role in addressing grand challenges in environmental stewardship. We examine the efforts of five Long Term Ecological Research Network sites to enhance policy, management, and conservation decisions for forest ecosystems. In these case studies, we explore the approaches used to inform policy on atmospheric deposition, public land management, land conservation, and urban forestry, including decisionmaker engagement and integration of local knowledge, application of models to analyze the potential consequences of policy and management decisions, and adaptive management to generate new knowledge and incorporate it into decisionmaking. Efforts to enhance the role of long-term research in informing major environmental challenges would benefit from the development of metrics to evaluate impact; stronger partnerships among research sites, professional societies, decisionmakers, and journalists; and greater investment in efforts to develop, test, and expand practice-based experiments at the interface of science and society.

Keywords: boundary spanning, environmental policy and management, Long Term Ecological Research Network, science communication

The growing urgency and complexity of challenges to global sustainability demands new approaches for engaging the intellectual capital of expert communities worldwide. To meet this demand, the scientific and social-science communities must expand their capacity to work at the interfaces between ecological science and environmental policy, natural-resource management, and conservation. The need for stronger, more-reliable linkages between science and society is well documented in both popular media and the academic literature (e.g., Lubchenco 1998).

The US National Science Foundation (NSF) recognized the importance of translating the benefits of research for society by establishing its “broader impacts” review criterion in 1997. In 2002, the NSF’s 20-year review of the Long Term Ecological Research (LTER) Network recommended that the LTER Network program assume a more powerful and pervasive role in informing environmental solutions at local, national, and international levels. In 2005, the Ecological Society of America (ESA) established the foundation for its Earth Stewardship initiative (Chapin et al. 2011) when it recommended that ecologists must play a greatly expanded role in communicating their research and influencing policies and decisions that affect the environment. It is critical for the LTER Network and for other ecosystem research programs to move beyond broad calls for action and to build deliberate and effective long-term relationships between ecological science and environmental decisionmaking. In this article, we illustrate, as do the other authors in this special section (e.g., Thompson et al. 2012 [in this issue]), the growing role that LTER is playing to enhance science engagement with local, regional, and national policy and management issues. To develop such programs, the scientific community needs to build experience and learn from practical examples of effective synthesis and integration of LTER to meet the needs of society. In this article, we present and discuss five case studies of work at the interface of science, policy, and management from forested LTER Network sites across the United States. We distill a set of common strategies, lessons, and recommendations for improving and expanding interface efforts to improve the ability to meet the grand challenges in environmental science of our time.

Effective science interface efforts

Although the integration of science and society is often viewed as a relatively narrow issue of a need for more and better science communication, programs that build stronger interfaces between science and society require attention to the full range of boundary-spanning activities, such as public engagement, decision-relevant synthesis, distillation of results, and science translation and dissemination, through
a variety of media to meet the needs of diverse audiences (Cash et al. 2003, Driscoll et al. 2011). Boundary spanning refers to “practices and processes that facilitate bringing science and society closer together in order to produce ‘useful’ information—that is, information that is salient, credible, and legitimate” (McNie et al. 2008, p. 9). Building credibility, salience, and legitimacy with stakeholders helps to solidify long-term relationships and increases the influence of scientific research in the decisionmaking process over time (Cash et al. 2003).

**The role of the LTER Network**

After 30 years of coordinated research and education, the LTER Network is well positioned to facilitate the integration of science and society by using its highly credible, long-term science to support engagement with decisionmakers to frame relevant questions for research and synthesis that can inform environmental policy and conservation. The LTER Network consists of 26 research sites throughout the United States and a few outside the United States, some of which have been operating for three decades or longer. The long-term ecosystem measurements and experiments that are a hallmark of the LTER Network address important environmental issues in coupled human–natural systems, including climate change, land use, pollution, and the loss of biodiversity (Knapp et al. 2012 [in this issue], Thompson et al. 2012 [in this issue]). Another distinguishing feature of the LTER Network is its core of researchers at each site, who are attentive to the well-being and future of their respective bioregions.

The LTER Network’s new Strategic Communication Plan (LTER Network 2010a) and Strategic and Implementation Plan (LTER Network 2010b) call for the network to reach out to decisionmakers at local, regional, national, and international levels. The communication plan specifically recommends engaging decisionmakers in the framing of cross-site synthesis and equipping these efforts with full-scale communication capacity, funding a supplement program for LTER Network sites to develop local and regional programs for public engagement and outreach, and partnering with existing LTER Network sites that have established science journalism programs to develop sustained outreach to the media.

**The value of long-term monitoring and research**

Environmental policy and management issues play out over decades or longer and benefit from the continuous advances in understanding that are derived from long-term research. Policy development is an iterative process that requires ongoing assessment, reevaluation, adaptive management, and consideration of future scenarios (Driscoll et al. 2010). For example, although the Clean Air Act was first passed by Congress in 1972, the development of amendments and rules to implement the act are ongoing and rely on quantitative information to evaluate the effectiveness of pollution-control measures and to guide program management (Lovett et al. 2007). Long-term measurements that link decreases in emissions with changes in soil and water quality and the health of aquatic and terrestrial ecosystems are vital to assessing the extent to which air pollution regulations meet the intent of the act (Driscoll et al. 2001).

Similarly, effective natural-resource management is adaptive and draws on lessons from past decisions and management experience distilled from the results of long-term measurements and experiments, regional surveys, and modeling (Spies et al. 2010). The practice of forestry in landscapes that support multiple uses must adapt to new knowledge regarding the nature and effects of climate change, forest management, land-use trends, intense storms, fire, and other disturbances. This understanding must include the impacts of these often interacting pulse and press stressors on management goals and ecosystem services, such as fiber production, biological diversity, carbon storage, trace-gas production and consumption, water quantity and quality, and recreation. Detailed, long-term measurements tied directly to management-relevant forest experiments have improved the scientific basis for forest management and policy. Important examples include the guiding principles for the conservation of old-growth forests (Franklin et al. 1981) and regional- and continental-scale carbon budgets important to climate-change mitigation (Lovett et al. 2007).

The five case studies presented here represent examples of outreach activities at selected forested LTER Network sites. We chose this suite of case studies because they have active programs for engaging decisionmakers, represent a range of policy and management issues, and use different approaches to achieve their outreach goals for a common ecosystem type. Reviewing efforts across forest sites provides the opportunity to consider how audiences, management and policy issues, and communication approaches vary across diverse regional research sites and programs. Specifically, the case studies incorporate the impacts of atmospheric deposition on forested ecosystems (Hubbard Brook), land-use change and forest conservation in a predominantly private-lands landscape (Harvard Forest), endangered species and public lands management (Andrews), urban forestry in developed landscapes (Baltimore), and forest stewardship in the context of changing fire and climate regimes (Bonanza Creek). These case studies represent only some of the many science–policy integration efforts that exist across the LTER Network (for other examples, see the Translating Science for Society brochure at http://intranet2.lternet.edu/sites/intranet2.lternet.edu/files/documents/Network_Publications/Brochures/nsf0533.pdf). In each of these cases, the ability to tap into core strengths of the LTER Network, such as long-term research that is relevant to policy and management issues, advanced information-management systems, and stores of long-term data, has proven essential to the synthesis and distillation of science for use in policy and management decisions related to coupled human–natural systems.
Case studies in linking LTER science with policy, conservation, and management

Below, we describe several case studies that link LTER science with policy, conservation, and management.

Air pollution effects on ecosystems: The Hubbard Brook Research Foundation Science Links Program. Air pollution can have marked effects on the structure and function of ecosystems through elevated atmospheric deposition of sulfur, oxidized and reduced nitrogen compounds and mercury, and high concentrations of tropospheric ozone. Recent efforts to channel this knowledge into decisionmaking through organized outreach and communication have increased the influence of long-term research on air-quality management in the United States (Driscoll et al. 2010). The LTER Network, through its long-term measurements and experiments (Driscoll et al. 2001), has been particularly effective in addressing policy issues concerning air pollution and atmospheric deposition effects on ecosystems.

The effects of air pollution on forest and aquatic ecosystems have been a research focus since the inception of the Hubbard Brook Ecosystem Study and the Hubbard Brook LTER site. The value of long-term measurements of the chemistry of precipitation and streamwater at the Hubbard Brook Experimental Forest in documenting trends in acidic deposition and in assessing the effectiveness of the federal Clean Air Act represents an important example of the connections between long-term research and air-quality policy (figure 1). The Hubbard Brook Research Foundation (HBRF) launched Science Links in 1998 to build on this legacy and to develop new initiatives linking ecosystem science with public policy (http://hubbardbrookfoundation.org/12-2).

Science Links projects are state-of-the-science synthesis efforts of an environmental issue in the context of current policy discussions. The first three Science Links projects addressed air pollution impacts on ecosystems, including the effects of acid, nitrogen, and mercury deposition (Driscoll et al. 2001, 2011). Science Links projects involve teams of around 12 scientific experts, selected on the basis of their experience and disciplinary coverage, and a team of policy advisers. The science teams define the scope of the project, analyze relevant databases and conduct model calculations. The policy advisers are engaged in dialogue from the outset to frame policy-relevant questions, discuss the alternatives analyzed, and provide input on Science Links products.

A communication and outreach plan is integral to the success of Science Links projects. The written plan provides a roadmap to facilitate an exchange between scientists and policy stakeholders as well as direct outreach to journalists. The centerpiece of any Science Links project is the translation report aimed at congressional and government-agency staff involved in policy development. These reports are structured to facilitate communication of the major findings, with the conclusions presented first in clear, straightforward terms, followed by supporting information with layered details. A proactive media strategy has been critical to the impact of Science Links projects. Accurate and widespread media coverage has brought attention to Science Links results and verified the societal importance of the findings for policymakers. The initial public release of a Science Links report is followed by additional interviews, seminars, and briefings for up to a year. Science Links projects have also been coupled with the Hubbard Brook LTER site educational activities through the development of supplemental teacher guides.

There are several dimensions to quantifying the impact of Science Links projects (Driscoll et al. 2011). The scientific impact can be measured by the number of citations in the scientific literature; the six Science Links journal articles have been cited more than 1300 times in the peer-reviewed literature. The media impact can be measured by the extent and quality of media coverage. Science Links initiatives have been covered in more than 475 media stories and have appeared in major news outlets, including an opinion-editorial piece in The New York Times. The impacts on policy are more difficult to quantify. Moreover, they are
often beyond the control of the scientists, regardless of the process used to link science to policy. Timing is everything in this dance between science and management. Forms of evidence of policy uptake include reference to Science Links findings in proposed legislation (e.g., the Clean Power Act, the National Mercury Monitoring Act), legal briefs (e.g., the Northeast States New Source Review case against the US Environmental Protection Agency), and media accounts of major policy and court decisions (e.g., the Interstate Transfer Rule for nitrogen oxide emissions and the remand of the Clean Air Mercury Rule and its trading provisions). Beyond this evidence, policymakers and program managers routinely comment on the usefulness of Science Links in improving the scientific basis for decisionmaking because of its reliance on rigorous long-term research and effective translation.

Uniting conservation science and policy: Examples from the Harvard Forest LTER site. The Harvard Forest has oriented its long-term studies around forest management and conservation questions in New England since its inception in 1907. When it was established by Harvard University, its objectives were to serve as a model forest to demonstrate the practice of forestry, an experiment station for research in forestry, and a field laboratory for students (Fisher 1921). Today, Harvard Forest scientists remain dedicated to the founding tenet of drawing on insights gained through the historical and retrospective study of forests, natural disturbance, and land use (Fisher 1933, Foster 2000), and the Harvard Forest serves as a central gathering spot for meetings and workshops among forest managers, conservationists, policymakers, and scientists in the Northeast.

Long-term research at Harvard Forest has informed many important conservation efforts, as well as policy and management decisions in the region (figure 2; Foster et al. 2010). For instance, a review of land-ownership history and conservation patterns led to the creation of the North Quabbin Partnership and to an increase of conservation...
land in the region from 36.8% in 1993 to 45.1% in 2010 (Golodetz and Foster 1997). Research on the potential for local constraints on forestry to displace harvesting pressures to other, more sensitive parts of the world has broadened public acceptance of forestry in the region (Berlik et al. 2002). Surveys have documented how underrepresented old-growth forests are in southern New England, which has aided in the preservation of the few remaining sites (Orwig et al. 2001, D’Amato et al. 2006). Many of these linkages grew out of strong informal ties between scientists and stakeholders built by serving on local, state, and regional committees.

In 2005, the Harvard Forest launched its Wildlands and Woodlands (W&W) Initiative, which emphasizes decision-relevant synthesis, communication, and stakeholder partnerships. The knowledge gained from dozens of studies at the Harvard Forest was synthesized into a series of W&W publications that were aimed at nonscientists and that called for stemming the loss of forest cover now occurring in all six New England states as large areas (e.g., in Maine) experience significant shifts in landownership. The publications call for balancing the preservation of wildlands with large areas of actively managed woodlands and for promoting civic engagement through landowner-conceived woodland councils (Foster et al. 2005, 2010).

Since 2005, the W&W Initiative has produced two major reports, two update publications, and a Web site (www.wildlandsandwoodlands.org), with the purpose of raising awareness about the pace and consequences of land-cover change. Both W&W reports had extensive stakeholder input, and the second garnered comments from several hundred agency, nongovernmental-organization (NGO), landowner, and industry representatives. Harvard Forest has since teamed up with the nonprofit organization Highstead to form a partnership with more than 60 participating groups to sustain stakeholder engagement and to help implement the vision of the W&W Initiative. The reports were accompanied by press releases; webinars; stakeholder briefings; and, in May 2010, a public event with Harvard University’s Kennedy School of Government.

Assessing the societal impact of Harvard Forest research over the past 100 years is beyond the scope of this case study. However, we compiled information on the impact of W&W communication to shed light on the value of this coordinated outreach effort. In the two months following its release, the 2010 report generated 137 media and newsletter stories and 62 visits per day to the new W&W Web site, including visitors from 35 countries from five continents. By contrast, Harvard Forest garnered 21 non-W&W news stories between 2008 and 2010. W&W authors participated in 21 briefings, presentations, and workshops in the nine months since publication, which expanded the project’s influence and reach. These W&W synthesis and communication efforts have contributed to several notable policy and management advances, including the decision by the state of Massachusetts to establish permanent wildland reserves, the introduction of a conservation-finance bill in the Massachusetts General Assembly to accelerate the pace of conservation, and the launching of an innovative effort to aggregate multiple parcels into a single project with the goal of conserving approximately 10,000 acres of forest in western Massachusetts. The W&W efforts also fueled new research, including the establishment of new long-term study plots across sites with diverse histories, ownership, and management objectives; and a new cross-site LTER proposal on the Future Scenarios of Forest Change (see Thompson et al. 2012 [in this issue]).

Sustained research–management partnerships at the Andrews Forest LTER site. The H. J. Andrews Experimental Forest and LTER site in the Oregon Cascade Range contains many of the iconic and hotly debated elements of Pacific Northwest forests: old-growth trees; northern spotted owls; and cold, clear, fast streams. Societal conflicts over the future of the vast tracts of federal forestlands in the region have been profoundly affected by science findings from the Andrews Forest and, in turn, have strongly influenced the course of science in the region and more broadly.

The research history of the Andrews Forest, stretching back to its establishment in 1948, reflects a commitment to long-term ecological and watershed research by the US Forest Service and with NSF-funded programs under the International Biological Program in the 1970s, followed by LTER Network since 1980. These integrated science programs have produced high-quality studies and long-term records that underpin interpretations of ecosystem and environmental change and sustain an interdisciplinary cadre of scientists, all of whom are essential in investigating ecosystems that change abruptly and also gradually over time scales of decades and centuries. The context of extensive federal forestlands (e.g., US Forest Service, US Bureau of Land Management) provides an audience of land managers who are required to guide management using current science. And, if they fail to do so, litigants and the courts remind them.

A central feature of the Andrews Forest program is a research–management partnership that develops, tests, demonstrates, and critically evaluates alternative approaches to management so that when the policy window opens, new, scientifically and operationally credible approaches to management are ripe for broad adoption (http://andrewsforest.oregonstate.edu/resmgt.cfm?topnav=35). This partnership involves the research community centered on the Andrews Forest LTER site and land managers of the Willamette National Forest. The partnership has made substantial impacts on forest management and policy on topics such as the characteristics and conservation strategies for old-growth forest ecosystems (Franklin et al. 1981, Spies and Duncan 2009); the ecological roles and management implications of dead wood on land and in streams (Gregory et al. 1991); the ecology and population dynamics of the northern spotted owl (Forsman et al. 1984); the effects of forest cutting and roads on streamflow, including floods (Jones 2000);
manifest in federal agencies’ management of forest stands and landscapes throughout the Pacific Northwest and more broadly (figure 3). In particular, the Northwest Forest Plan, which drew heavily from research from the Andrews Forest, ushered in a new era of ecosystem-based management on 10 million hectares of federal lands in northern California and western Oregon and Washington (FEMAT 1993, USDA and USDI 1994). Andrews Forest–based science on old-growth forests, forest–stream interactions, aspects of biodiversity, and the roles of dead wood in forests and streams helped shape new federal land-management policies (FEMAT 1993). Several of the key publications have been cited in the scientific literature more than 1000 times each, which indicates the influence of the concepts in the environmental sciences. Since 1994, individual research themes have continued to influence management practices in the region (figure 3). Publications from the Andrews Forest–based work are widely cited in planning documents for timber sales and fuel-treatment projects on National Forests and US Bureau of Land Management districts across the Pacific Northwest. The impact of the research–management partnership has drawn social scientists to examine the dynamics, motivations, and public perception of these science–management–policy connections (Lach et al. 2003).

**Figure 3. Andrews Experimental Forest research and links with management and policy for forestlands and watersheds.**

interactions of road and stream networks (Jones et al. 2000); and interactions of climate change with management and policy (Spies et al. 2010).

With roots in the early 1950s and the assignment of the first scientist to the Andrews Forest, the research–management partnership has become a continuous, place-based learning program with balanced, reciprocal communication between the management and research communities and their respective cultures. To facilitate communication, the research–management interface is staffed with a research liaison position at the Willamette National Forest, which facilitates outreach to land managers and the public. The technical findings of research and management experience are communicated through diverse media, such as journal articles, including ones jointly composed by scientists and land managers (Cissel et al. 1999); publications prepared for land managers and the general public (e.g., in the *Science Findings* and *Science Update* series of the US Forest Service; www.fs.fed.us/pnw/publications/sci-fi.shtml, www.fs.fed.us/pnw/publications/sci-update.shtml); workshops; and field tours. In some cases, social scientists have examined the effectiveness of communications on challenging topics, such as the use of historic disturbance regimes to guide future land management (Shindler and Mallon 2009). The net effect of this communication program is a continuing public discussion of the future of forest and watershed management and policy in the region.

The impacts of long-term research from the Andrews Forest and the research–management partnership are manifest in federal agencies’ management of forest stands and landscapes throughout the Pacific Northwest and more broadly (figure 3). In particular, the Northwest Forest Plan, which drew heavily from research from the Andrews Forest, ushered in a new era of ecosystem-based management on 10 million hectares of federal lands in northern California and western Oregon and Washington (FEMAT 1993, USDA and USDI 1994). Andrews Forest–based science on old-growth forests, forest–stream interactions, aspects of biodiversity, and the roles of dead wood in forests and streams helped shape new federal land-management policies (FEMAT 1993). Several of the key publications have been cited in the scientific literature more than 1000 times each, which indicates the influence of the concepts in the environmental sciences. Since 1994, individual research themes have continued to influence management practices in the region (figure 3). Publications from the Andrews Forest–based work are widely cited in planning documents for timber sales and fuel-treatment projects on National Forests and US Bureau of Land Management districts across the Pacific Northwest. The impact of the research–management partnership has drawn social scientists to examine the dynamics, motivations, and public perception of these science–management–policy connections (Lach et al. 2003).

**Tools for assessing services and values to improve urban natural-resources stewardship: Baltimore Ecosystem Study long-term data.** Information on natural resources in urban areas is often lacking and limits the ability of planners and managers
to properly steward or incorporate natural-resources services within urban ecosystems. Long-term research is currently being conducted in the Baltimore area to foster a better understanding of how urbanization affects natural system processes (e.g., Pickett and Cadenasso 2006). Baltimore, through its participation in the LTER Network, was one of the first cities to have its entire forest and tree structure assessed, along with the concomitant ecosystem services and values (e.g., pollution removal, carbon storage and sequestration, effects on building energy use; see, e.g., Nowak et al. 2008). It is also the first city (along with Syracuse, New York) to establish (in 1999) permanent vegetation-monitoring plots to assess long-term vegetation changes (Nowak et al. 2004). These data provide critical information for better understanding of urban vegetation systems, their environmental effects, and how these ecosystems are changing. These data have also helped in the development and testing of public-domain software tools designed to aid managers and the general public in assessing urban trees and their associated ecosystem services and values. Data collected in Baltimore and other cities in the mid to late 1990s led to the development of software to assess urban forest structure and functions: the UFORE (urban forest effects) model (Nowak and Crane 2000). Through time, a diverse collaboration developed among numerous partners to expand the development of this and other urban forest computer programs into a suite of free software tools known as i-Tree (www.itretools.org), which was released in 2006.

The information provided by i-Tree software has been used to inform management and policies throughout the world in relation to urban forestry. The influence of i-Tree results from the use of the model and local data by consultants, managers, and local citizens to guide management and policies decisions related to issues such as emerald ash borer protection (Siyver 2009), building financial support for urban forestry programs (Society of Municipal Arborists 2008), linking local tree data with the US Conference of Mayors Climate Protection Agreement (Hyde 2009), public outreach campaigns (e.g., billboards) on the benefits of trees (Siyver 2009), developing urban forest strategic management plans (McNeil and Vava 2006), and helping secure financing for tree planting and management (e.g., Ibrahim 2009). Most of the data collected and analyzed through i-Tree are used to properly steward or incorporate natural-resources services within urban ecosystems. Long-term research is currently being conducted in the Baltimore area to foster a better understanding of how urbanization affects natural system processes (e.g., Pickett and Cadenasso 2006). Baltimore, through its participation in the LTER Network, was one of the first cities to have its entire forest and tree structure assessed, along with the concomitant ecosystem services and values (e.g., pollution removal, carbon storage and sequestration, effects on building energy use; see, e.g., Nowak et al. 2008). It is also the first city (along with Syracuse, New York) to establish (in 1999) permanent vegetation-monitoring plots to assess long-term vegetation changes (Nowak et al. 2004). These data provide critical information for better understanding of urban vegetation systems, their environmental effects, and how these ecosystems are changing. These data have also helped in the development and testing of public-domain software tools designed to aid managers and the general public in assessing urban trees and their associated ecosystem services and values. Data collected in Baltimore and other cities in the mid to late 1990s led to the development of software to assess urban forest structure and functions: the UFORE (urban forest effects) model (Nowak and Crane 2000). Through time, a diverse collaboration developed among numerous partners to expand the development of this and other urban forest computer programs into a suite of free software tools known as i-Tree (www.itretools.org), which was released in 2006.

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Information and results from i-Tree, its analyses, and impacts are generally communicated by the research partners and users to others through public presentations, reports and articles, webinars, the i-Tree Web site, and word of mouth. To assist in communicating project results, i-Tree automatically produces a standard report with graphics that users can export and customize for their own use (figure 4). Users can also report ideas, questions, or problems back to the i-Tree team, which are then used to update or develop future versions.

To date, more than 8200 unique users in 99 countries have downloaded the software. Use of i-Tree has grown at about 30% per year since its release in August 2006. i-Tree Web site traffic has increased about tenfold since the release of version 3.0 in June 2009 and continues to increase. Currently, about 20,000 unique users access the Web site every three months. Focused surveys of users have been conducted to help determine the types of impacts. Between 50 and 100 journal articles and reports have been published in which i-Tree was used, and the numbers have increased annually. New programs in development are focused on temporal and spatial modeling of forest effects, and the Baltimore long-term permanent field-plot data are critical to the development of these new tools. International urban forest data standards are also in development to aid in sharing and in the use of the programs among nations.

**Climate-change impacts on wildfire: Bonanza Creek engagement with fire managers and indigenous communities.** Alaska is warming twice as quickly as the global average, with little change in precipitation (Chapin et al. 2006a). The resulting drying of the boreal forest has increased the annual area burned, primarily through increased frequency of dry years and larger wildfires, which have important consequences for changes in forest cover and the closely coupled human and ecological communities (figures 5 and 6; Kofinas et al. 2010). Bonanza Creek scientists collaborate with fire managers and indigenous communities to share knowledge for predicting and adapting to changing fire regimes.

Working with fire managers, Bonanza Creek LTER ecologists have developed predictive models that provide a scientific foundation for fire-management decisions. Spatially explicit models of climate and wildfire suggest that, by 2050, a “typical” fire year in interior Alaska will be similar to the most extreme fire years in the historical record (www.snap.uaf.edu). These models were developed through extensive input from climatologists, ecologists, and fire managers (Duffy et al. 2005).

At the community level, village tribal councils have invited Bonanza Creek ecologists to collaborate in developing new ecosystem-management strategies to respond to increasing wildfire risk. These strategies include the sustainable harvest of flammable black spruce stands near communities to heat public buildings, create new jobs, and generate secondary successional habitat that favors moose—an important food source (Chapin et al. 2008, Kofinas et al. 2010). Bonanza Creek social scientists and ecologists have also participated in federally mandated community wildfire protection planning by conducting interviews and focus groups among local residents and resource managers. These interviews
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The Bonanza Creek LTER site is forging new ground in identifying climate-change impacts that require immediate management and community action. The associated metrics of impact are therefore recent and qualitative. Judging from the ESA’s Sustainability Science Award for Chapin and colleagues’ (2006b) article, in which they described the socio-ecological framework for this research, the Bonanza Creek LTER site is contributing to fundamental science and to new approaches for integrating community knowledge and concerns in socioecological research (figure 6). Bonanza Creek collaborations contributed to Alaska fire managers’ capacity to adapt federal guidelines on the basis of fire issues of the lower 48 US states to conditions and issues that are relevant to Alaska. Managers use the fire-risk model and routinely invite Bonanza Creek ecologists to participate in the training of wildfire managers, which indicates that they value the practical relevance of LTER. Bonanza Creek ecologists and Alaskan indigenous leaders have formed the Working Group demonstrated that local residents trusted managers to plan community-level wildfire protection but felt disenfranchised in regional wildfire planning for the surrounding lands, because their knowledge and concerns about future subsistence opportunities and places of cultural value were overlooked (Ray 2010).

Fire-modeling results are communicated to fire managers and the public through participation in annual wildfire strategic-planning workshops, agency meetings with the public, joint agency LTER planning of prescribed burns, and production of site-specific 2-kilometer-resolution climate projections and fire-risk projections on request (www.snap.uaf.edu).

Community workshops coorganized by tribal councils and Bonanza Creek ecologists allow an exchange of local, traditional, and scientific knowledge about wildfire ecology. This dialogue has enriched understanding by the LTER scientists of the ecological and societal consequences of climate change. The trust that develops through community partnerships enables Bonanza Creek researchers to learn from and contribute to societal responses to a rapidly changing socioecological environment.

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Figure 4. Example of the user interface for i-Tree. The page shows the i-Tree canopy survey page for urban forests.
on Rural Alaska Self-Reliance, a collaboration to implement community visions of adaptation to global change. This collaboration suggests that indigenous leaders value and trust their interactions with Bonanza Creek scientists.

**Discussion of the case studies.** Boundary-spanning efforts can facilitate the bridging of science and society by producing information that is salient, credible, and legitimate (Cash et al. 2003, McNie et al. 2008), which ultimately enriches scientific research through stakeholder engagement, the expansion of public awareness, and the improvement of the scientific basis for decisionmaking. The five LTER case studies presented here offer experiences and lessons to help answer the question of what characterizes successful collaborative outreach efforts. The case studies suggest that efforts to build a stronger interface between science and society are shaped in part by three overarching attributes that pertain to all ecosystems but vary in detail among ecosystems: (1) **Landscape and social context** refers to the pattern of land ownership (e.g., private versus public) and the role of the different types of knowledge (e.g., local versus expert) that influence the framing of environmental issues, the management objectives, and the science used in the decisionmaking process. (2) **Issue definition** involves determining the relevance of particular long-term research to policy and management issues at local, regional, or national scales (e.g., local fire- or fuel-management issues, regional air-quality concerns, federal forestland policy) and the extent to which individual actions or government actions are central to resolving the issues of concern. (3) **Communication pathways** entail understanding which communication approaches are most appropriate for specific decisionmakers, and the choice of pathway is determined in part by the context and issues addressed (e.g., direct briefings between scientists and policymakers; outreach to the media; working groups with managers; discussions with local communities, including tribes).

In addition to these three overarching attributes that distinguish individual efforts, a set of common elements of successful science communication efforts emerges from the case studies:

- **Landscape and social context**
- **Issue definition**
- **Communication pathways**

In all of the case studies, boundary-spanning efforts were built on credible, multidecade, interdisciplinary science, and peer-reviewed publications. These efforts combine retrospective analysis; long-term measurements and experiments; quantitative modeling; and, increasingly, scenarios planning. For example, the ability of the HBRF Science Links projects to assess the impacts of air-quality regulations and the extent...
to which ecosystems have recovered was entirely dependent on the existence of long-term precipitation, soil and stream chemistry, and relevant biological measurements. These data enabled scientists to analyze changes in atmospheric deposition and associated chemical and biological responses, to establish impact thresholds, and to apply dynamic models to evaluate the extent to which future emissions reductions would achieve policy objectives.

Among the most important activities is the collaboration of scientists and decisionmakers at the outset of and throughout a research effort. This interaction helps to define issues and questions salient to decisionmakers, to identify sources of knowledge beyond traditional scientific data sets, and to envision outputs that best meet user needs. This process also enriches scientific research. For example, the Bonanza Creek research framework was expanded through interactions with community groups to larger temporal and spatial scales and integration of cultural dimensions. This led to the recognition of critical thresholds of the resistance of the boreal socioecological system to climatic and socio-economic changes.

Although scientists are accustomed to publishing focused research in peer-reviewed publications, these case studies point clearly to the need for policy- and management-relevant synthesis and distillation to support the effective use of science in the policy and management processes. This problem-oriented synthesis is necessary but not sufficient for promoting knowledge sharing and should be accompanied by work to translate the key findings into compelling terms relevant to stakeholders. For example, by pulling together disparate findings from across dozens of articles produced over a decade or more, the Harvard Forest W&W publications have drawn public and stakeholder attention to that body of work and catalyzed conservation initiatives far beyond what any single study could accomplish.

Successful outreach should not be an afterthought but a major and well-funded initiative with adequate staffing and supporting expertise ranging from traditional print publications to media, including Web-based, outreach. Innovative online tools that promote interaction and social networking and that are open source and easily accessible are increasingly important communication vehicles. For example, the i-Tree project built a program interface that is easy to use, open to all, supported, and free: The i-Tree partnership has built a platform to which others can contribute, and new peer-reviewed tools can be added and then supported through the existing i-Tree partnership and model structure.

Partnerships are critical to sustaining reciprocal flow of information among scientists, citizen leaders, managers, and policymakers; to applying scientific findings to policy and management through an adaptive process; and to fueling processes in which stakeholder experiences and knowledge inform research. For example, the research–management partnership developed by the Andrews LTER site and the US Forest Service provides a platform for sustained, place-based learning with substantial attention to communications with many audiences. Similarly, the Baltimore LTER i-Tree project also functions as a partnership that meets regularly and has open discussions, working toward meeting the needs of the urban community. In both cases, the involvement of a public entity (the US Forest Service) has been instrumental in coordinating and managing the activities of the partnerships.

In addition to these lessons, the case studies presented here demonstrate the need for stronger metrics to measure the impact of science communications and outreach to decisionmakers. In general, metrics for evaluating public-engagement outreach efforts can be divided into three categories: output, uptake, and impact. The five case studies
present outputs such as the number of publications and presentations given to nonscientific audiences. They also provide strong evidence of uptake such as media coverage, scientific citations, and Web site visitation. Quantifying the impact on policy, conservation, and stewardship decisions remains elusive.

Developing and applying meaningful metrics of impact is a common challenge. Under the auspices of the White House Office of Science and Technology Policy, the National Institutes of Health and the NSF are developing metrics of impacts for science, called STAR METRICS (Science and Technology for America’s Reinvention: Measuring the Effects of Research on Innovation, Competitiveness, and Science; Lane and Bertuzzi 2011). Several metrics have been proposed to measure the usefulness of scientific knowledge, many of which are applied in these case studies (e.g., download or hit rates, media coverage, citations in federal or state regulations). But in the area of broader impacts or social outcomes, such as those in health, safety, and the environment, recommendations are under development by an interagency working group. Impact metrics for science are an important gap in understanding that should be remedied by the STAR METRICS program and other science-policy research efforts.

Conclusions

If science is to aid in the advance toward a more resilient and sustainable society, we must experiment with more effective means of integrating ecological research and decision-making. As is evidenced by the five case studies presented here for forest ecosystems and by many other examples, the LTER Network has an important and unique role to play in addressing the grand challenges in environmental and sustainability science. The LTER Network and associated research, with its long-term interdisciplinary focus, its focus on place-based study, its geographic distribution, its sophisticated information-management systems, and its public-outreach capabilities, are well suited to boundary-spanning initiatives that address emerging environmental issues related to changes in biogeochemistry, biological diversity, climate change, ecohydrology, infectious disease, and land use. Policy-relevant synthesis and science communication should be a focus of the LTER Network, and these activities, in turn, would probably promote cross-site and network-wide coordination of matters important to both science and society. This work could be enhanced by partnerships with established scientific societies that are dedicated to similar work. For example, the ESA is advancing a partnership among academic societies, agencies, and NGOs “to foster Earth Stewardship by (a) clarifying the science needs for understanding and shaping trajectories of change at local-to-global scales; (b) communicating the basis for Earth Stewardship to a broad range of audiences, including natural and social scientists, students, the general public, policymakers, and other practitioners; and (c) formulating pragmatic strategies that foster a more sustainable trajectory of planetary change by enhancing ecosystem resilience and human well-being” (Chapin et al. 2011, p. 45).

Harnessing the power of long-term ecological studies to address the grand challenges in environmental science will require learning from and building on existing efforts to better integrate scientific research with societal concerns. The NSF can facilitate this process by expanding the bounds of informal education to include the engagement of decisionmakers and journalists in order to provide the requisite research and learning needed to develop, test, and expand these critical experiments at the interface of science and society.

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Scenario Studies as a Synthetic and Integrative Research Activity for Long-Term Ecological Research

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Scenario studies have emerged as a powerful approach for synthesizing diverse forms of research and for articulating and evaluating alternative socioecological futures. Unlike predictive modeling, scenarios do not attempt to forecast the precise or probable state of any variable at a given point in the future. Instead, comparisons among a set of contrasting scenarios are used to understand the systemic relationships and dynamics of complex socioecological systems and to define a range of possibilities and uncertainties in quantitative and qualitative terms. We describe five examples of scenario studies affiliated with the US Long Term Ecological Research (LTER) Network and evaluate them in terms of their ability to advance the LTER Network’s capacity for conducting science, promoting social and ecological science synthesis, and increasing the saliency of research through sustained outreach activities. We conclude with an argument that scenario studies should be advanced programmatically within large socioecological research programs to encourage prescient thinking in an era of unprecedented global change.

Public investment in science increasingly comes with the expectation that research will address the complex challenges that society faces and will contribute to strategies that sustain the vitality and integrity of socioecological systems (Reid et al. 2010). During the past 30 years, as the US National Science Foundation (NSF)–sponsored Long Term Ecological Research (LTER) Network has grown from 6 to 26 research sites, ranging from Alaska to Antarctica and from urban ecosystems to forests to coral reefs. The LTER Network has increasingly used innovative approaches to connect science to society: from direct engagement with policymakers to educational programs in public schools and software applications that inform the public about the structure, function, and state of socioecological systems (Bestelmeyer et al. 2005, Driscoll et al. 2012 [in this issue], Robertson et al. 2012 [in this issue]). Scenario studies are one such approach and are emerging as a powerful tool for synthesizing the results of LTER science and for engaging with stakeholders to consider socioecological futures. There is a rich history involving the use of scenarios to encourage prescient thinking, largely born out of military and corporate planning (Kahn 1962, Wack 1985). Scenarios offer a framework for practitioners to integrate diverse modes of knowledge and to explicitly recognize those components of complex systems that are understood and those that are uncertain. In this way, scenario studies can describe multiple ways in which our shared socioecological future may unfold, sometimes including a visioning process that is focused on the specific attributes of one preferred future condition. Although the first type of scenario studies yield impartial descriptions of a range of possible future states, visioning describes desirable future states (or visions)—for instance, according to sustainability principles or stakeholder agreement (Swart et al. 2004, Carpenter and Folke 2006, Weaver and Rotmans 2006). Both types of scenario are contrasted with probability-based approaches to forward-looking research below.

We refer here to scenario studies in general as any strategy for describing plausible future conditions while explicitly incorporating relevant science, societal expectations, and internally consistent assumptions about major drivers, relationships, and constraints (Xiang and Clarke 2003, Iverson Nassauer and Corry 2004, Raskin et al. 2005, Bolte et al. 2007, Mahmoud et al. 2009). Unlike predictive modeling, scenario studies acknowledge the uncertainty inherent in socioecological systems and therefore do not attempt to forecast the precise or probable state of any variable at a given point in the future. Instead, comparisons among a set of contrasting scenarios are used to understand the systemic interrelation and dynamics of complex socioecological systems.
and to define a range of possibilities and uncertainties in quantitative and qualitative terms. The value of scenario studies lies in the process of embedding alternative states of the future into a transparent problem-solving framework (Swart et al. 2004). In this way, scenario studies may help to anticipate change in systems characterized by high levels of irreducible uncertainty and low levels of controllability (Bennett et al. 2003, Peterson et al. 2003a) and evoke new integrative perspectives and novel concepts of ecological change (Carpenter and Folke 2006, Carpenter et al. 2006). Although environmental scenarios are developed for a wide range of specific purposes, scenario studies can serve three widely accepted functions: education and public information, scientific exploration, and decision support and strategic planning (Alcamo and Henricks 2008, Henrichs et al. 2010).

In many large science- and environmental-assessment programs, scenarios have been used to describe and underpin analyses of alternative futures. The Intergovernmental Panel on Climate Change’s (IPCC) emission scenarios (Nakićenović and Swart 2000) and the Millennium Ecosystem Assessment’s scenarios (MA 2005) are perhaps the most well known, but there are many others (e.g., Sala et al. 2000, Raskin et al. 2005). Several LTER sites, for example, are deeply involved in scenario studies and even more plan to be. A recent LTER Network–sponsored workshop brought together 32 social and ecological researchers representing 16 LTER sites from around the United States that were actively engaged in some aspect of scenario studies for the region surrounding their sites (Thompson and Foster 2009). The participants reaffirmed what may seem self-evident: LTER-based science has several characteristics amenable to developing regional socioecological scenarios. Credible socioecological scenarios require a deep understanding of long-term environmental dynamics—a signature strength of LTER science—and a tight coupling of ecological and social research—an emerging strength of and direction for the LTER Network (Collins et al. 2011, Robertson et al. 2012 [this issue]).

Looking forward to the next 30 years of LTER—and, more generally, to other research programs concerned with understanding socioecological systems—we argue that the application of scenario studies can advance prescient thinking in an era of unprecedented rates of global change. For example, an overarching goal set forth in the LTER Network’s Strategic and Implementation Plan is to use its deep understanding of complex socioecological systems to help anticipate ecological, evolutionary, and social responses to future environmental change and to inform societal strategies to adapt to this change (LTER Network 2011). This aligns seamlessly with the primary functions of scenario studies (i.e., underpinning decision processes, collaborative learning, and scientific exploration). More specifically, scenarios can enable site-based research programs to explore possible as well as desirable and sustainable future states of their respective regions. And through sustained partnerships with land managers, policymakers, and other stakeholders, participatory scenarios can increase the societal relevance of their research. Moreover, in scenario studies in which the socioecological future of their regions is formally considered, new research needs can be identified while research in temporal and spatial dimensions is scaled up. Finally, developing and analyzing future scenarios would provide a platform for working with many scientific networks, including the National Ecological Observatory Network (NEON) and Urban Long Term Research Areas (ULTRA).

Driscoll and colleagues (2012) explore the novel ways in which scientists have delivered their research findings to policymakers and managers where they can inform decisions. They describe several important communications approaches that allow new science to span boundaries and to address new challenges. In the present article, we examine scenario studies as one such boundary-spanning approach, using several examples of scenario studies from LTER sites in order to identify approaches that may be more broadly applicable. More specifically, we evaluate one emerging and four mature scenario studies in terms of three questions that address the value of scenarios for advancing socioecological science, programs, and outreach:

A science question: How do the scenario studies relate the past to the future? Related to this question are those of what attributes of the socioecological system will change a lot, what attributes will change a little, and why. To articulate a range of alternative futures in a plausible and credible manner, it is necessary to understand the relevant history and trajectory of environmental and social change of the system of interest and its component parts. Evaluating future scenarios in light of recent changes, then, leads to an understanding of system attributes that are more or less resilient or vulnerable to future change. This feature of scenario studies is especially valuable as socioecological change approaches “tipping points” and the need to anticipate and mitigate future change becomes acute (Scheffer et al. 2001, Rockström et al. 2009).

A programmatic question: How do the scenario studies relate to the more traditional long-term science occurring within LTER? Related to this question is how they can advance science synthesis. Scenarios take many forms and, as is shown below, they may have narrow or expansive thematic scope. But in all the case studies, scenarios are either informed by or are used as a platform for applying the core long-term research coming from the individual LTER sites. Consequently, scenarios can be a compelling approach to science synthesis and for cross-site comparative analyses.

An outreach question: How do the scenario studies affect the region and regional society through real-world changes or capacity building? Future scenarios draw together stakeholders affected by the hypothesized future changes. By engaging
in scenario studies, scientists can place themselves in a new relationship with society. It can be a means for linking science and decisionmaking in order to support future and hopefully sustainable trajectories for socioecological systems, whether they are wild landscapes, natural resource lands, or urban areas.

Case studies
The case studies showcase diverse ways in which scenario studies are being employed as a vehicle to understand the drivers of socioecological change, to engage with regional stakeholders, and to consider shared socioecological futures. Each is distinct in its motivation, methodology, and outcomes. To provide a consistent organization for evaluation, we describe each using a seven-part conceptual framework (figure 1, table 1) that includes (1) a trigger or context (i.e., what precipitated the study and in what environment [e.g., academic, professional] it occurred), (2) a goal (i.e., what the leaders and participants in the scenario study hoped to achieve), (3) construction or methodology (i.e., what scenario construction method was used), (4) collaboration (i.e., who was involved in scenario development [e.g., regional or national stakeholders, experts]), (5) scenarios (i.e., what scenarios [i.e., topics] were generated and what the mode or representation [e.g., narratives, visuals, maps] was), (6) use (i.e., in what ways the scenarios were used after they were completed [e.g., research, planning and decisionmaking, education and training]), and (7) impacts (i.e., what social impacts the application of the scenarios yielded [e.g., it improved the network, influenced policy decisions, changed professional practice, or increased capacity]).

**Figure 1.** Analytical framework for evaluating diverse forms of scenario studies conducted throughout the US Long Term Ecological Research Network.
<table>
<thead>
<tr>
<th>Project Title, LTER site, space, and record length</th>
<th>Triggers and context</th>
<th>Goals</th>
<th>Method (1) and steps (2)</th>
<th>Collaboration</th>
<th>Scenarios: topic (1) and format (2)</th>
<th>Uses</th>
<th>Impacts</th>
</tr>
</thead>
<tbody>
<tr>
<td>North American Forest Scenarios LTER sites: Harvard Forest, Coweeta, NTL, AND, BNZ Space: 15 landscapes / 5600–27,000 km² Time: 50 years forward</td>
<td>1. Academic 2. Identify regional characteristics that alter continental-scale drivers of global change</td>
<td>1. Create contrasting scenarios 2. Provide input for cross-site LTER comparative research</td>
<td>1. Elicit narratives 2. Parameterize interactive simulation models</td>
<td>Input from national and regional stakeholders</td>
<td>1. Forest conversion, energy production, climate mitigation, conservation, etc. 2. Narratives (technical), maps, graphs, visualizations</td>
<td>This is an emerging project whose use and impacts have yet to be realized.</td>
<td></td>
</tr>
</tbody>
</table>
Overall, the process of scenario planning increased the connectivity of the NTL group to other groups actively engaged in the region. The process also had the immediate effect of increasing the extent of networking among diverse stakeholders who had long histories in the NHLD but little prior interaction. This connectivity improved the outreach capacity of the NTL and introduced the science to more potential users.

**Blue River Landscape Plan and Study scenarios: The Andrews Forest LTER site.** In the early 1990s, forest policy in the Pacific Northwest abruptly shifted from several decades of management in which commodity (timber) production was emphasized to one that was focused on species conservation (Duncan and Thompson 2006). The Northwest Forest Plan (NWFP) was the policy instrument that codified this change. The NWFP was itself the product of a scenario approach in which scientists, including several from the Andrews Forest (AND) LTER site, prepared 10 management scenarios (alternatives) for the Clinton administration (FEMAT 1993), with one selected as the basis of the NWFP. Within the plan, 10 large parcels (40,000–200,000 hectares) of federal forestlands were delineated as adaptive management areas (AMAs), in which scientists and land managers were charged with examining alternative strategies to meeting conservation and timber-production goals. At the Central Cascades AMA, which contains the AND site, LTER scientists teamed with land managers of the Willamette National Forest to construct a landscape-scale forest-management plan. They used science-based visioning to describe an ecologically desirable but unconventional approach to long-term management that was informed by historic fire regimes and landscape dynamics rather than by standard reserve-design criteria. The resulting scenario, called the Blue River Landscape Plan and Study (BRLP; Ecoshare 2011), patterned timber harvests on the historical wildfire regime (Cissel et al. 1999). The BRLP’s resulting “disturbance-based” or “historical range of variability” approach began with a dendrochronology-based fire-history study that spanned the previous 500 years (Weisberg 1998), which was used to semiquantitatively generate a map of three fire-regime types distinguished by fire frequency and severity and constrained in part by topography. A forest planner used this fire-regime map and a map of the then-present distribution of forest age classes to project harvests 200 years into the future. The plan included novel approaches to individual-tree and patch retention and to cutting-rotation length to emulate the historical wildfire severity and frequency. This disturbance-based approach to landscape management was contrasted with expected future management under the NWFP, which is based on the management of unharvested reserves and matrix land (i.e., actively harvested areas between reserves), for its conservation value for selected species (Cissel et al. 1999). Public reaction to the disturbance-based plan was assessed through surveys and field-tour discussions. The public had a significant level of acceptance, although the concept and vocabulary were unfamiliar to many (Shindler and Mallon 2009). The BRLP has since served as an actual management plan intended for implementation, as well as a demonstration project used for critical discourse within science, land-management, and public circles. The BRLP helped reveal to the various stakeholders that an understanding of natural-disturbance regimes can lead to a viable approach to harvesting and the conservation of biodiversity and ecosystem functions. Lessons being learned from the BRLP have been widely communicated and may be used for new applications as society charts the management of public lands through a dynamic future socioecological system (Spies and Duncan 2009).

**Future vision and scenarios for Phoenix: Central Arizona–Phoenix LTER site.** In autumn 2009, the city of Phoenix, the Central Arizona–Phoenix (CAP) LTER site, and the School of Sustainability at Arizona State University initiated a research project entitled “The Future of Phoenix: Crafting Sustainable Development Strategies.” (Wiek et al. 2012). The purpose of the combined visioning and scenario study was to create—through a collaboration of expert facilitators, scientists, and stakeholders—a vision and contrasting scenarios that captured a spectrum of possible future developments of Phoenix. The vision described Phoenix as a desirable and sustainable socioecological system, as was determined by stakeholder agreement and sustainability principles (Gibson 2006). The contrasting scenarios described alternative—less desirable and less sustainable—future states and represented what might happen if the vision is not achieved (Withycombe and Wiek 2011). In the vision that resulted from this participatory research process, Phoenix was described as being comprised of vibrant communities, where healthy food, clean water, fresh air, excellent educational opportunities, satisfying jobs, and public transit options are available to all citizens; where strong local businesses take advantage of local assets to build a diverse and community-oriented urban economy; where governance is open and transparent and reflects the values of all people, regardless of their power or influence; and where the urban ecological system is preserved and cared for, so that it can be sustained for generations to come. In the contrasting scenarios, two alternative future states of Phoenix are described: Phoenix behind the times, in which the city acknowledges critical challenges from climate change to environmental degradation and social tensions but cannot seem to keep pace with other regions in creating a healthy socioecological system, and Phoenix overwhelmed, in which the city ignores long-term challenges, upholds the growth paradigm, and continues to overextend its capacities and to jeopardize sustainable future development pathways. The vision was presented in three formats: stories with photographs, a narrative, and a map of priorities. The scenarios were presented as newspaper cover pages with illustrations and as narratives. Visioning and scenario construction combined several methods, such as consistency analysis, diversity analysis, sustainability appraisal, and trade-off analysis.
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(Wiek et al. 2006, Withycombe and Wiek 2011). In the study, the knowledge, preferences, and values of a broad range of experts and regional stakeholders were elicited, deliberated, and integrated. The core stakeholder-engagement activities were 15 meetings in all parts of the city, designed to elicit vision statements, and a visioning workshop, in which the elicited vision statements were revisited, systemically linked, and reprioritized on the basis of potential conflicts. More than 100 citizens, city planners, business representatives, nonprofit organization members, and researchers participated in this workshop. The vision and the scenarios are now being used by the city administration in planning, training, and fund raising, as well as for teaching purposes in public schools and at Arizona State University. Overall, the project spurred a rich public discussion about the future directions in which Phoenix may be headed and about the degree to which these directions align with a desirable and sustainable future vision. The substance of the vision and scenarios has been incorporated into the current public-hearing draft of the city’s general plan (City of Phoenix 2010), which is the city’s most important guide for long-term planning and development. It provides direction for planning and allows researchers, policy analysts, and stakeholders to evaluate the effectiveness of policies and actions.

The Scenarios Network for Alaska Planning: The Bonanza Creek LTER site. Arctic and boreal forests are warming about twice as fast as the global average, creating widespread concern and interest in the patterns and consequences of climate change, especially among northern residents. At the Bonanza Creek (BNZ) LTER site, scenarios have been used as both a research and a communications tool to explore the consequences of recent and projected climate change in Alaska. Rapid change experienced in Alaska has focused public attention on these scenarios, which in turn has led to the establishment of a research partnership: the Scenarios Network for Alaska Planning (SNAP; www.snap.uaf.edu), which comprises the BNZ, the University of Alaska, and several state and federal agencies, local communities, and nonprofits. SNAP has developed scenarios of future climate as high-resolution maps of mean monthly historical and projected temperature and precipitation (between 1900 and 2100) that account for the known effects of topography and the movement of air masses. By downscaling the five global circulation models that were shown to perform best in the far north and by providing outputs for three emission scenarios defined by the IPCC, SNAP offers stakeholders a range of possible climate futures, rather than a single prediction. Moreover, discussion and interpretation of uncertainty play a large role in SNAP projects. The actual technical work of downscaling the climate scenarios is an expert-driven process. However, all SNAP projects are collaborations between SNAP researchers and land managers or other stakeholders. These stakeholders help determine how the data will be linked to landscape models, existing data sets, and local knowledge and how the resulting scenarios will be used and interpreted. For example, in collaboration with US Fish and Wildlife Service, The Nature Conservancy, and other partners, SNAP researchers have used climate-change scenarios to model potential biome shifts and changes in the ranges of endemic and invasive species. In the resulting report (Murphy et al. 2010), barren-ground caribou, Alaska marmots, trumpeter swans, and reed canary grass were used as indicator species to assess multiple possible futures, given the possible range of climate-change impacts. In addition, the climate scenarios have been used directly by Alaska communities in order to inform decisionmaking about the future sustainability of hydroelectric generation and other energy project plans (Cherry et al. 2010).

The American Forest Futures Projects: The Harvard Forest, Andrews Forest, Bonanza Creek, Coweeta, and North Temperate Lakes LTER sites. Scenario planning is the focus of American Forest Futures Projects, an emerging group of cross-site LTER projects that are being advanced across the major forested regions of the United States in collaboration with major NSF-sponsored programs (including, e.g., five LTER Network sites, NEON, ULTRA), the US Forest Service, the US Geological Survey, the Smithsonian Institution, and several NGOs (e.g., The Nature Conservancy, the Ecological Society of America, the Heinz Center). The projects were designed to address pressing scientific questions related to how and why forested regions vary in their socioecological responses to global change (www.wildlandsandwoodlands.org/node/133). In a parallel thrust, the researchers designed the projects as a means to advance several burgeoning network-level LTER Network priorities, such as national- and regional-scale stakeholder engagement, development of models and visualization tools, and communication with policymakers. The projects rely on tiered scenarios developed at national and regional scales to address at least four dominant themes: economic development, energy exploitation (e.g., bioenergy), climate mitigation and adaptation, and landscape-scale conservation.

The researchers have convened a national advisory board of experts, consisting of federal agency and national NGO representatives, to develop national-scale scenarios describing the anticipated drivers and the changes associated with each of the themes. After they are finalized, the suite of national-scale scenarios will be interpreted at regional scales around the country by engaging regional stakeholders (e.g., natural-resource managers, scientists, agency officials, conservation professionals) in the development of narratives in which the local manifestation of each of the national scenarios is described. This process of downscaling global scenarios to local scales can be an effective approach for participatory capacity building and for motivating behavioral changes in local stakeholders and decisionmakers (Shaw et al. 2009). The regional scenarios will, in turn, be used to define land-use assumptions and to parameterize spatially interactive landscape-simulation models (e.g., Thompson et al. 2011) within study a series of study landscapes.
(5600–27,000 square kilometers) dispersed throughout five forest regions: the Northeast, the Lake States, the Southeast, the Pacific Northwest, and Alaska. Using the scenarios and simulation outputs, the group plans to conduct a series of within- and across-region comparisons to evaluate how ecosystem attributes and services change in response to similar national scenarios of global change along multiple social and ecological gradients, including productivity and topography, land tenure and demographics, land-use history and policies, disturbance regimes, and climate. This approach for coupling qualitative and quantitative scenarios has informed prescient planning and policy and has generated a rich set of fundamental research questions (see, e.g., Spies et al. 2007, Schmitt Olabisi et al. 2010). Although it is still in its early stages, the American Forest Futures Projects have already spurred dialogue among dozens of agencies and stakeholder groups in an effort to describe an envelope of plausible futures for forested landscapes across the country.

Discussion of the case studies

From these case studies, we offer responses to our initial three questions:

How do the scenario studies relate the past to the future? Unlike predictive modeling, in scenario studies, no level of confidence is asserted that any particular changes will occur. Instead, several possible changes are integrated into a set of potential future pathways in which the major drivers are logical and consistent across scenarios. In doing so, scenario studies provide useful contexts for addressing questions about how past change may or may not help understand future change, given a range of possible societal dynamics (e.g., population growth, shifting demographics, land-use change) and possible environmental dynamics (e.g., climate, invasive species, major disturbance events). The BRLP, for example, was based on the concept that important elements of the future will represent an extension of historic trajectories of change and also incorporated a detailed understanding of historic landscape change over many centuries in response to disturbance by wildfire, flood, and landslides. The future landscape is expected to include continued responses of forest and stream systems to those past disturbance regimes, as well as future regimes resulting from direct and indirect human influences and natural processes. The vision of management based on historical ecosystem dynamics acted as a medium for discussing these complexities among scientists, land managers, and the public. By examining a range of plausible futures, scientists and stakeholders could consider the range of social and ecological uncertainty and learn about the attributes that drive change, even if they do not know exactly what level of change will occur. The value of considering how historical trends may diverge along multiple alternative pathways was also evident in the NHLD, where big shifts in the status quo were foreseen from both internal and external forces. Internally, concern was focused on political gridlock and a lack of capacity to make collective decisions. Externally, concern was focused on the demographic and economic drivers of massive development in the Northern Highland. These internal and external social drivers were thought to affect the resilience of the region to climate change and other biophysical drivers. In the NHLD scenarios that were seen as optimistic by most respondents, the social and political system of the region changed in ways that facilitated resilient responses to large-scale biophysical changes.

Evaluating multiple scenarios that are informed but not constrained by history can have great advantages over the predictive modeling of future conditions, which can pose serious challenges even in seemingly straightforward analyses and when long-term data exist. For example, we live in a period of high concern over climate change, yet in many cases, climate-change signals are difficult to interpret amid the temporal variability of climate at multiple temporal scales, even with 50-year historical records (Jones et al. 2012 [in this issue]). In Alaska, where the impacts of climate change have been felt by communities for many years, gathering information about how land managers and residents are experiencing and reacting to change offers crucial information about how to address future change. Those who are living with changes, such as increased fire risk, treeline shift, or severe coastal erosion, can offer information about how these changes are already being experienced and managed and can make specific requests about what kind of climate information and what models would be most useful. The SNAP scenarios span a range of potential climate futures, informed by the best available science, but without the false precision of predictive models. The climate scenarios can, in turn, be integrated into socioecological models and narrative stories that define potential futures in a way that managers and residents can relate to and plan for. The use of scenario studies is therefore a productive means for relating historical landscape change to forward-looking analyses of unpredictable socioecological systems.

How do the scenario studies relate to the more traditional long-term science occurring within the LTER Network? Scenario studies are often a form of synthesis of both biophysical and social science. Framing plausible alternative depictions of the future and evaluating them promotes highly integrative thinking. The social, political, and land-management contexts in which LTER sites are embedded increasingly demand a level of integrated analysis that is uncommon in traditional scientific research but that is central to scenario studies. In each of the case studies, the strengths of traditional LTER science—notably, monitoring and evaluating the impacts of long-term environmental change—were integrated into the scenario studies. For example, in the American Forest Futures Projects, the future response of forest ecosystems to climate and land-use change are evaluated over time using ecosystem-process models that are developed and constrained by LTER. National and regional stakeholders define the narratives that guide their assumptions about land use
and other societal responses, thus linking the scenarios to the legacy of “hard science” traditionally upheld by LTER. Likewise, in Alaska, where climate change is a topic that has reached a relatively high level of public awareness, SNAP and the BNZ are already engaged in the type of synthesis that forges connections between LTER and exogenous social and economic pressures. In working with groups such as the National Park Service, the Fairbanks North Star Borough Climate Change Task Force (www.investfairbanks.com/Taskforces/climate.php), and Alaska’s governor’s Subcabinet on Climate Change (www.snap.uaf.edu/projects/governors-subcabinet-climate-change-0), SNAP has received input from partners who are concerned about the interplay among multiple ecological factors in the context of budgets, short planning cycles, and public criticism. Scenario planning has proven to be a useful tool in this context, because it allows scientists to offer the best available information in a way that incorporates uncertainty and that allows planners to assess risk on their own terms.

Importantly, in all of the case studies discussed here, knowledge transfer and syntheses flowed in both directions, whereby the science informed the scenarios and, in turn, the scenarios informed the science. For example, within the NTL program, the scenarios contributed to a shift toward explicit long-term thinking about socioecological change that has influenced research and the planning of site activities. Recent projects have been focused on thresholds for abrupt change in fisheries, food webs, and invasive-species dynamics, for example. Climate change has been a long-standing interest at the NTL that is also serving as an organizing focus for hypothesis-driven long-term research. Similarly, the Future Vision and Scenarios for Phoenix study serves as a pilot project and will be continued with even more emphasis on the integration of previous CAP work. To this end, a formal synthesis workshop will be conducted in order to make the links to the other CAP working groups explicit and to plan future contributions. The study has also been proven to stimulate collaboration between CAP researchers and other research groups at Arizona State University that are already engaged or interested in scenario studies in the CAP region (across different spatial levels and topic areas).

How do the scenario studies impact the region and the regional communities through real-world changes or capacity building? Scenario studies are a distinctive form of science engagement with society and one that has only recently been employed in LTER. They are much more participatory than traditional outreach that consists of a delivery of scientific findings to policymakers, managers, and the public. For example, the Future Vision and Scenarios for Phoenix study has served as a powerful medium to enhance the engagement between CAP researchers and regional stakeholders. Although CAP research has included stakeholder engagement since its inception in 1997, the dominant mode of operation has been one-way elicitation. The scenario study, in contrast, has demonstrated how more interactive engagement can enhance the interest and ownership for the challenges as well as potential solutions across different stakeholder groups. The ongoing scenario work further expands the participatory-research methodology through advanced collaborative visualization, walking audits, and exploration courses. Similarly, the BRLP scenario has proven to be very useful process for generating discussion among varied stakeholders—pro- and antilogging groups alike—of the dynamics of forest ecosystems and the relevance of natural variability for future management. Having a management scenario based on historic disturbance regimes has fostered public understanding of landscape dynamism at a time when some elements of the public seek to freeze components of the landscape as though it were a museum diorama.

LTER scenario studies have also led to novel uses of technology to engage the public. Taking just a few examples from the case studies, the American Forest Futures Projects are developing a Web-based course modeled after the highly successful LTER Network-sponsored “From Yardstick to Gyroscope” class (http://news.lternet.edu/article170.html), in which the science of scenario studies will be taught to university students and landscape planners. As part of the BNZ SNAP project, a Web-based community charts tool has been developed (www.snap.uaf.edu/community-charts) that allows Alaska residents to compare a range of possible future climate scenarios for their own village (from among more than 350 in the state) and a Google Earth interface (www.snap.uaf.edu/google-earth-maps) that lets users zoom in on their own region and define which models they would like to explore. At CAP, as part of the Future Vision and Scenarios for Phoenix study, the Decision Theater at Arizona State University is to be used to evaluate the effectiveness of those participatory processes for capacity building and decisionmaking.

Overall, the scenario studies presented here demonstrate how considering our shared socioecological future can motivate sustained engagement between science and society. We believe that the long-term dimension of the US LTER Network makes it a highly suitable venue for scenario studies. Indeed, the 30-year history of the LTER program provides time for development of social networks with key parts of society (e.g., decisionmakers, NGOs, government agencies with lands responsibilities, interested members of the public). Finally, members of the LTER Network’s science community live and work in their studied landscapes and are themselves stakeholders with a deep personal stake in its future.

Conclusions
As the case studies show, scenarios can be an effective approach for synthesizing science in a major research program and can lead to an improved understanding of socioecological change. Scenario studies offer a flexible framework for integrating the best available ecological
science with the myriad of uncertainties that are inherent in global change. Using scenarios, large ecological research programs, such as the LTER Network, NEON, and ULTRA, can lead societal discussion regarding the future of their landscapes. The core strengths of the LTER Network in particular—its history of long-term, place-based studies; its community of scholars committed to integrative research across disciplines and service to society; and its diversity of landscapes, stakeholders, and disturbance regimes—make it ideally suited to leading scenario studies in each of the landscapes in which LTER sites are present. As such, we suggest that scenario studies be advanced in collaboration with many other research groups and agencies as a network-wide activity to promote research in socioecological systems and cross-site comparative analyses across the network.

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Past, Present, and Future Roles of Long-Term Experiments in the LTER Network


The US National Science Foundation–funded Long Term Ecological Research (LTER) Network supports a large (around 240) and diverse portfolio of long-term ecological experiments. Collectively, these long-term experiments have (a) provided unique insights into ecological patterns and processes, although such insight often became apparent only after many years of study; (b) influenced management and policy decisions; and (c) evolved into research platforms supporting studies and involving investigators who were not part of the original design. Furthermore, this suite of long-term experiments addresses, at the site level, all of the US National Research Council’s Grand Challenges in Environmental Sciences. Despite these contributions, we argue that the scale and scope of global environmental change requires a more-coordinated multisite approach to long-term experiments. Ideally, such an approach would include a network of spatially extensive multifactor experiments, designed in collaboration with ecological modelers that would build on and extend the unique context provided by the LTER Network.

Keywords: climate change, global change, long-term research, LTER Network, multifactor experiments

More than 30 years ago, Odum (1977) described ecology as a uniquely integrative and synthetic scientific endeavor, and the diversity of research approaches employed today reflects this perspective (e.g., Rees et al. 2001). Collectively, ecologists conduct research that includes virtually every ecosystem type on Earth, with studies that span a broad range of spatial and temporal scales. Moreover, the most successful research programs generally employ a mixture of complementary approaches, including retrospective studies, observations, experiments (natural and manipulative), gradient studies, synthetic analyses, and modeling. The research portfolios of the 26 sites within the US National Science Foundation (NSF)–funded Long Term Ecological Research (LTER) Network (http://lternet.edu) exemplify this spatially and temporally extensive and multifaceted approach to ecology (Hobbie et al. 2003), although the degree to which the sites allocate time and resources to particular research approaches varies on the basis of the questions being addressed, site-specific constraints, and the culture of the discipline (e.g., oceanographers study systems differently than do forest ecologists).

Site-based manipulative experiments have long been a cornerstone of ecological research. Although long-term experiments (box 1) have a foundational history in ecology (e.g., the Rothamsted fertilization study begun in 1856), short-term experiments are much more common for a variety of reasons (Tilman 1989). Short-term experiments provide information on how a system is regulated at the time and place of the manipulation (i.e., the initial limiting factors and their interactions). However, in complex systems with multiple components operating on different time scales of response, the initial trajectories of response of either the whole system or of individual components (e.g., single species) will not necessarily indicate either the direction or the magnitude of long-term change. Long-term experiments, when coupled with measurements of key processes, will be more likely to enable interpretation of the entire trajectory of system response, as well as the trajectories of change in system components (i.e., species or pools of organic matter and elements). A key difference between long-term and short-term experiments is that long-term experiments provide insight into the causes of the changes in the slope of responses, the causes of the inflection points, and the magnitude of the long-term change, whereas short-term experiments are focused only on the initial trajectories. Thus, long-term experiments can address mechanisms and temporal dynamics in a complementary fashion, particularly when the experiments are combined with other research approaches (e.g., observational and gradient studies). In doing so, they can help elucidate how historical influences
Early long-term experiments of the LTER Network

Long-term experiments served as the basis for the establishment of the research programs at several of the initial LTER sites funded in the 1980s. For example, the AND, CWT, and HBR LTER sites (see table 1 for site abbreviations) began as US Department of Agriculture (USDA) Forest Service experimental forests. At these sites, the responses of hydrology, energy flow, and nutrient cycling to changes in forest structure caused by disturbance had been quantified experimentally using paired watersheds (e.g., Hewlett and Helvey 1970) and the small-watershed approach (Likens 1985) for a number of years prior to their being included in the LTER program (figure 1). Similarly, the USDA Agricultural Research Service established long-term livestock grazing experiments at several of their experimental ranges in the early 1900s, two of which became LTER program sites (JRN and SGS; see figure 1). The response of arctic tundra vegetation to long-term manipulations of nutrient availability and temperature (Chapin et al. 1995) also provided the foundation for continuing studies of global-change effects at the ARC site (figure 1).

Research programs at several other founding LTER sites were built around newly established long-term experiments designed to test a diverse set of hypotheses, with the expectation of a long-term funding commitment. For example, the role and mechanisms whereby soil resources regulate community structure have been examined in plot-level manipulations at the CDR site since its inception (figure 1). The long-term consequences of nitrogen (N) deposition, climate warming, and hurricanes for nutrient cycling, carbon (C) dynamics, and forest productivity have been assessed at HFR (Foster et al. 1997). Moreover, experiments evaluating the interactions of fire, ungulate grazing, and climate variability in driving patterns and processes in tallgrass prairie formed the basis for long-term experiments at KNZ (figure 1). Finally, the core experiment in row-crop agriculture at KBS involved the long-term imposition of a gradient of varying management inputs into midwestern US cropping systems.

In all cases, the expectation that key ecological responses to these manipulations might not become evident for many years justified the long-term nature of the experimental design for these LTER programs.

Long-term experiments today in the LTER Network

In order to provide a more comprehensive overview of long-term experiments in the LTER Network, we surveyed each of the 26 LTER sites (table 1) to quantify the number, types, and durations of long-term experiments supported by the LTER Network. In addition, we convened a two-day working-group meeting with participants from of a subset of LTER sites in February 2011. On the basis of responses (from 100% of the sites) to the survey questions, a total of 239 long-term experiments (completed and ongoing) were identified within the LTER Network (table 1). Of these, less than 10% exceed 30 years in duration, which indicates that most long-term experiments were initiated during the time frame of the LTER Network (figure 2). Diversity among the
although long-term experiments related to infectious disease are notably underrepresented (figure 2). Finally, a majority of the sites (16 of 26) participated in multisite or network-level experiments (i.e., experiments that spanned multiple sites), which may or may not have included other LTER sites. Notable examples include the Nutrient Network, the Long-Term Intersite Decomposition Team (LIDET), and the International Tundra Experiment.

Our assessment of long-term experiments during the working-group meeting revealed that many of the earliest long-term experiments were designed as single-factor manipulations with the goal of gaining an improved understanding of the long-term nature of change (primarily at the process level) in response to either short-term (pulse) or long-term (press) manipulations. In the early years of LTER, assessing recovery from disturbance using pulse experiments

<table>
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<tr>
<th>Site name</th>
<th>Site acronym</th>
<th>Year established in LTER Network</th>
<th>Number of long-term experiments</th>
<th>Number of multifactor experiments</th>
<th>Multisite experiments (yes [y] or no [n])</th>
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<tr>
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<td>1980</td>
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<td>2004</td>
<td>1</td>
<td>1</td>
<td>n</td>
</tr>
<tr>
<td>Niwot Ridge</td>
<td>NWT</td>
<td>1980</td>
<td>8</td>
<td>6</td>
<td>y</td>
</tr>
<tr>
<td>North Temperate Lakes</td>
<td>NTL</td>
<td>1980</td>
<td>6</td>
<td>2</td>
<td>n</td>
</tr>
<tr>
<td>Palmer Station</td>
<td>PAL</td>
<td>1991</td>
<td>0</td>
<td>0</td>
<td>n</td>
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<tr>
<td>Plum Island Ecosystems</td>
<td>PIE</td>
<td>1998</td>
<td>3</td>
<td>2</td>
<td>y</td>
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<tr>
<td>Santa Barbara Coastal</td>
<td>SBC</td>
<td>2000</td>
<td>1</td>
<td>0</td>
<td>y</td>
</tr>
<tr>
<td>Sevilleta</td>
<td>SEV</td>
<td>1988</td>
<td>12</td>
<td>3</td>
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</tr>
<tr>
<td>Shortgrass Steppe</td>
<td>SGS</td>
<td>1981</td>
<td>17</td>
<td>4</td>
<td>y</td>
</tr>
<tr>
<td>Virginia Coast Reserve</td>
<td>VCR</td>
<td>1987</td>
<td>4</td>
<td>1</td>
<td>y</td>
</tr>
</tbody>
</table>

Note: The principal investigators (PIs) were asked to provide information about long-term ecological experiments (as defined in box 1) at their site. Among other questions, the PIs were asked to report the number of long-term experiments, the number of experiments that included more than one manipulated factor, and if any of these long-term experiments were conducted at multiple sites. Additional results from this survey are provided in figure 2 and in the text.
(i.e., a single perturbation or manipulation event) was the most common type of experiment (Callahan 1984), such as deforestation studies at HBR and CWT or wind-disturbance studies at HRF. These studies were motivated by the need to develop or test theory in order to enable a deeper understanding of the ways in which key drivers altered ecosystem structure and function. The goal was to complement historical observations with knowledge and insight that were unattainable from traditional short-term experiments and space-for-time studies. Other experiments were initiated to understand the impacts of anthropogenic disturbances such as logging, grazing, and acid deposition. Although the initial focus was on disturbances, the more-recent trend is for long-term experiments to have stronger relevance to global-change drivers or to be linked explicitly to policy and major issues in natural-resource management (figure 3). The working group concluded that, given the number and diversity of long-term experiments in the LTER Network, Callahan’s (1984) vision of the LTER Network as one that could address the “serious contradiction between the time scales of many ecological phenomena and the support to finance their study” (p. 363) has been fulfilled.

**Synergies between the LTER Network and long-term experiments**

Although long-term experiments have been supported by many other programs and have been conducted successfully at a wide range of sites around the globe, long-term experiments conducted at LTER sites have many important advantages. First, long-term measurements at LTER sites provide essential context for interpreting experimental responses. Long-term observations can also provide pre-treatment and reference-system data, as well as the basis for identifying ecological surprises, such as extreme climatic events (Lindenmayer et al. 2010, Smith 2011). Such data are critical for interpreting experimental results over...
a background of natural variability—for separating signal from noise; however, these data sets are usually impossible to maintain through typical funding programs. At the HBR site, for example, researchers were able to quantify the magnitude of soil calcium (Ca) depletion caused by twentieth-century acid deposition only through 40 years of continuous biogeochemical measurements (Likens et al. 1996). These observations, in turn, inspired a long-term experiment in which soil Ca availability was returned to preindustrial levels (figure 3), with the long-term trajectory of forest biomass and demography providing the context for interpreting responses to the experimental treatment. The dramatic recovery of growth, health, and regeneration of sugar maple (Acer saccharum) in response to a moderate increase in soil Ca provided further evidence that human-induced soil Ca depletion has caused widespread decline in this highly valued forest tree and in forest productivity overall (Juice et al. 2006). In this case, the deployment of a highly sensitive tracer in the Ca treatment provided additional insights into the pathways of Ca flux through forested watersheds (Dasch et al. 2006).

In addition to long-term observations revealing patterns and inspiring experimentation to elucidate mechanisms, post-experiment monitoring at LTER sites can improve understanding and prompt the design of new studies (Janzen 2009). For example, a decade following the cessation of 10 years of experimental N additions at the CDR site, species richness had recovered, whereas other aspects of community structure had not. This led to a short-term experiment in which the manipulation of soil N availability, plant litter, and seed dispersal revealed the mechanisms related to recovery from chronic N fertilization (Clark and Tilman 2010). Similarly, ecosystem recovery was monitored for 10 years following 6 years of experimental acidification of Little Rock Lake (part of the NTL site) in northern Wisconsin (figure 3). This monitoring revealed that total zooplankton biomass recovered in one year, but community composition exhibited sustained differences. Approximately 40% of zooplankton taxa exhibited a lag in recovery after pH returned to the levels at which a biological response was first observed (Frost et al. 2006). Continued monitoring of the recovery of this system revealed complex trophic interactions and hysteresis effects—responses that would not have appeared with only a year or two of post-treatment measurements. Such opportunities arise because LTER Network sites provide consistent access to instrumentation and infrastructure, stable funding levels, and well-trained personnel who are available to continue the measurements. Furthermore, the information-management capabilities of LTER Network sites ensure that data will be collected using consistent protocols and will be archived and readily available for use by other researchers (Ingersoll 1997). Easily accessible data with well-documented metadata facilitate cross-site comparisons that are integral for expanding the results of experiments to broader spatial scales.
The value of long-term ecological experiments

On the basis of the working-group meeting and the broader site survey, we highlight below the diverse array of insights and contributions provided by long-term ecological experiments within the LTER Network. Our goal is to extend our review beyond the core scientific benefits of this suite of studies to include unique opportunities and broader impacts afforded by these long-term experiments.

Insights into long-term responses. Obviously, but not trivially, one of the greatest scientific benefits of long-term site-based experiments is that they elucidate how ecological systems respond to experimental treatments over the long term. Indeed, such experiments have repeatedly demonstrated that long-term responses to treatments can differ markedly from short-term responses (Tilman 1989, Debinski and Holt 2000). For example, in the BioCON experiment at the CDR site (biodiversity, CO₂, and N are manipulated; see figure 3), Reich and colleagues (2006) tested the hypothesis that the availability of N would constrain the response of productivity in an N-poor grassland community to elevated CO₂. Although this hypothesized interaction between N and CO₂ eventually became apparent, it was not until the fourth year of treatment. If the experiment had been discontinued before the fourth year (i.e., within the time frame of typical funding cycles), researchers might have concluded that N availability had no effect on the response of these communities to elevated CO₂. Similarly, in a manipulation of soil temperature at the HFR site (figure 3), the conclusion regarding the influence of warming on soil respiration would have been very different had the experiment ended after its first few years (figure 4). In that experiment, warming strongly increased...
soil respiration (by about 25%) in the first five years of the study (Melillo et al. 2002). However, by the tenth year of treatment, the warming stimulation had declined to less than 5% above ambient controls. Conclusions based on the initial results of this experiment would have led to an overestimate of the positive feedback to climate warming resulting from enhanced soil organic matter decomposition. Elucidation of the mechanisms underlying these responses was made possible by coupling these single-factor studies with those in which soil and N were simultaneously manipulated, whereas additional microbial studies enhanced ecosystem-scale understanding (Contosta et al. 2011).

Occasionally, experimentally induced shifts in ecosystems can take years to appear, which can lead to ecological surprises (Lindenmayer et al. 2010), as exemplified by the long-term phosphorus (P)—addition experiment conducted at the Upper Kuparuk River, Alaska (part of the ARC site). In this case, although P fertilization stimulated epilithic algal production immediately, a major increase in bryophyte production (with subsequent effects on nutrient cycling and higher trophic levels) became apparent only after a decade of treatment—a response that was completely unexpected (figure 5; Slavik et al. 2004). In other instances, the lack of response even after a decade or more of treatments may lead to an important new understanding of patterns and processes. For example, inspired by the dramatic response of desert grasslands to an exclusion of small mammals in Portal, Arizona (e.g., Brown and Heske 1990), replicate small mammal exclosures were established in a number of grassland and shrubland sites, including the SEV site. Although no significant differences in vegetation composition and dynamics have been observed to date at the SEV site (cf. Báez et al. 2006), major changes have occurred in other arid-land ecosystems (Meserve et al. 2003). The differences in responses among sites reflect the degree to which top-down control of community structure can vary among arid-land ecosystems and can prompt new experiments to better understand context dependence in the function of communities and ecosystems.

Besides elucidating how ecological responses to experimental treatments can change over time, long-term experiments can provide unique opportunities to uncover the mechanisms underlying such dynamics. In some instances, initial system responses may be dominated by the disturbance associated with initiating an experiment or because of
legacies of pretreatment conditions. Therefore, it may take a while before system responses are indicative of ecological processes. For example, patterns of nitrate loss from agricultural systems that vary in management intensity are notably variable, in part because many studies are initiated before treatments have fully equilibrated or are conducted over relatively short periods of time. This has led to widely conflicting reports and little agreement about the best management practices to decrease nitrate loss. In contrast, the long-term cropping systems experiment at the KBS site (figure 3) has enabled comparisons of nitrate losses from conventional, no-till, low-input, and organic cropping systems. Each of these treatments had six years to equilibrate before measurement, and they have been assessed for 11 years, which accounts for interannual variability (Syswerda et al. 2008). This study has revealed consistent and marked differences in nitrate losses, with the low-input and organic systems having about half the nitrate losses of the conventionally managed systems.

Long-term experiments can reveal the importance of indirect effects in ecosystem processes not apparent in the short term, as well as responses that may change over the long term (Tilman 1989). At the NTL site, the experimental acidification of a small seepage lake (figure 3) produced numerous changes driven by indirect interactions related to changes in the food web rather than by direct consequences of lower pH. For example, the rotifer Keratella taurocephela has displayed low acid tolerance in laboratory studies but increased in density throughout the acidification experiment as a result of decreased invertebrate-predator abundance (Gonzalez and Frost 1994). Keratella taurocephela also underwent morphological changes in the acidified basin as a result of reduced predation pressure. Responses driven by food-web interactions were often the opposite of expectations based on laboratory studies of pH tolerance and generally exhibited a time lag; these unexpected results would not have been observed on time scales shorter than the response time of all trophic levels.

**Other opportunities from long-term experiments.** Unavoidably, long-term experiments occur against a backdrop of long-term trends; stochastic ambient conditions, including climate variability and extremes and infrequent disturbances; and changes in the abundances of predators and pathogens at scales greater than the experimental units. Although the inability to control ambient conditions can be challenging, variability in background conditions can sometimes also prove fortuitous (Tilman 1989). For example, long-term experiments can be particularly valuable if they coincide with climate or weather extremes that provide new ecological understanding. Of course, the longer an experiment is conducted, the greater the chances that ambient conditions will vary in ways that produce insights and even inspire new experiments. During the Ca-addition studies at the HBR site (figure 3), an intense ice storm damaged sugar maple trees, which allowed researchers to document improved wound repair as one of the major responses to the alleviation of Ca deficiency and, presumably, a principal mechanism underlying increased growth rates (Huggett et al. 2007). At the CWT site, Yeakeley and colleagues (2003) designed an experiment to investigate the importance of riparian Rhododendron species to nutrient export to streams. They instrumented treatment and reference hillslopes, made two years of pretreatment measurements, and then removed all Rhododendron stems from a 10-meter (m) strip along 30 m of stream. Less than two months later, Hurricane Opal downed most of the large trees on the reference hillslope. Over the course of the study, they found that the hurricane impact on canopy trees had far greater effects on nutrient export than did the experimental Rhododendron removal. Finally, a wildfire at the KNZ site in 1996 reset most of the long-term fire treatments in the 60 watersheds at the site (figure 1) by burning them all on the same date. This afforded the opportunity to sample a large number of sites affected by the same fire but with a wide array of longer-term fire histories. This sampling revealed the importance of the amount of time since a prior fire in determining aboveground net primary productivity responses to fire (figure 6) and helped researchers interpret results from other experiments regarding the role of soil N in postfire responses (Blair 1997, Knapp et al. 1998).

Scientists conducting long-term experiments can also take advantage of dramatic changes in community structure, such as those resulting from extirpation or biological invasion. For example, at the KBS site, long-term monitoring of predaceous lady beetles (Coccinellidae) in experimental agricultural treatments has revealed three exotic species additions since 1988, including the multicolored Asian lady beetle (Harmonia axyridis). The arrival of the soybean aphid (Aphis glycines) in 2000 reunited these two Asian species in a new context and resulted in surprising dynamics. Prior to 2000, H. axyridis was a common species; however, after 2000, it became dominant (figure 7). Moreover, it demonstrated classic predator–prey cycling with high abundances following years of aphid outbreak (Heimpel et al. 2010); process-level studies demonstrated strong top-down control of A. glycines by coccinellids (Costamagna and Landis 2006). A further surprise was that biological control of the soybean aphid was regulated by the structure of the surrounding landscape: Suppression was positively correlated with landscape diversity at the 1.5-kilometer scale (Gardiner et al. 2009).

Finally, long-term experiments can provide opportunities to address novel questions that were not part of the original motivation for the experiment. Long-term N-enrichment studies at the ARC site were initiated as part of a broader suite of treatments designed to assess resource limitation and the response of tundra ecosystems to global-change factors (figure 1; Chapin et al. 1995). After 20 years of adding N, the researchers shifted their focus toward asking how much of the cumulative N added still remained in the plots and how this affected C pools (Mack et al. 2004). Somewhat surprisingly, these plots had lost significant C, despite greater C inputs (net primary production) and aboveground C stocks with N addition. Net
achieve general, synthetic understanding of ecological processes. Such studies can identify important influences on ecological processes at large spatial scales. They are more powerful than ad hoc meta-analytical syntheses, because they can eliminate variation in experimental methodologies across sites. For example, the LIDET studied long-term decomposition (10 years) by deploying common substrates across 27 sites, including 16 LTER Network sites (Harmon et al. 2009). The LIDET experiment yielded new insights into decomposition processes including a new understanding of the rates and controls of decomposition of more slowly decomposing litter fractions. Such insights would have been difficult to derive from the meta-analysis of published decomposition studies because most of those studies last one year at most and because substrate variability confounds site-to-site variability in factors such as climate (Adair et al. 2010).

Long-term experiments also take on added value when they inform and are informed by ecological theory and models. Tilman's (1982) study of resource competition that developed the resource-ratio hypothesis of competitive interactions was enriched by the close interplay between long-term experiments and the development of theory at the CDR site. Similarly, empirical research on resource limitation at the ARC site has occurred in close connection with the development of theory on multiple-resource limitation of ecosystem processes.

Broader contributions of long-term experiments. Beyond the basic ecological understanding that results from individual experiments, long-term experiments can be valuable by contributing to synthetic activities, testing and inspiring ecological theory and models across systems, and informing policy and management. With respect to synthesis, combining the results of multiple studies in meta-analyses or data syntheses can elucidate how factors such as climate, species composition, and edaphic conditions interact with treatments to influence ecological responses, which adds value to the original, individual experiments. For example, although numerous studies have demonstrated declines in plant species richness in response to N addition, synthesis of such results across a number of LTER sites revealed that the relative magnitude of species loss varied greatly across sites; warmer sites and those with high cation-exchange-capacity (CEC) soils exhibited lower declines in richness than sites that were colder or had low CEC (Clark et al. 2007). Sites with high abundance of C₄ grasses had a greater productivity response to N addition than did other sites, which was in turn associated with greater proportional declines in species richness.

Long-term experiments conducted at multiple sites, although less common, are particularly powerful ways to achieve general, synthetic understanding of ecological processes. Such studies can identify important influences on ecological processes at large spatial scales. They are more powerful than ad hoc meta-analytical syntheses, because they can eliminate variation in experimental methodologies across sites. For example, the LIDET studied long-term decomposition (10 years) by deploying common substrates across 27 sites, including 16 LTER Network sites (Harmon et al. 2009). The LIDET experiment yielded new insights into decomposition processes including a new understanding of the rates and controls of decomposition of more slowly decomposing litter fractions. Such insights would have been difficult to derive from the meta-analysis of published decomposition studies because most of those studies last one year at most and because substrate variability confounds site-to-site variability in factors such as climate (Adair et al. 2010).

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Multiple-resource-limitation theory, in turn, has influenced the development of Earth-system models that explore the implications of N constraints on C cycling at a global scale (e.g., Gerber et al. 2010). Given the number and diversity of long-term experiments in the LTER Network, the opportunity certainly exists for additional theory and model development capable of linking a broad array of patterns and processes across temporal and spatial scales.

There are broader practical outcomes of many long-term experiments when they influence the design of policy and management strategies. For example, the litter-exclusion experiment at the CWT site (figure 3) clearly demonstrated the importance of tree-leaf litter to the organisms living in headwater streams (Wallace et al. 1997). The importance of maintaining the integrity of headwater streams has been used as an argument against mountaintop mining practices in the central Appalachian region (Meyer and Wallace 2001) and cited in court cases (e.g., P. C. Chambers, US District Judge, Memorandum Opinion and Order on Civil Action No. 3:05-0784 in the Huntington Division of the US District Court of the Southern District of West Virginia, 23 March 2007). Experimental demonstration of the dramatic impacts of deforestation on soil and surface-water chemistry at the HBR site (Bormann et al. 1974) raised awareness of the consequences of intensive forest harvest for environmental quality and influenced the development of best management practices for these forests. Simulations of hurricanes and mortality resulting from pests and pathogens demonstrated that the ecosystem consequences of salvage and restoration management of forests—both post-windstorm and in advance of insect infestation or disease—are often much greater than the impacts of the disturbances themselves and led to the argument that leaving forests alone is often a viable management alternative from an ecological perspective (Foster and Orwig 2006). Finally, the results from long-term experiments, coupled with gradient studies, field observations, and data from monitoring networks, have been used to estimate the critical loads of N for freshwater and terrestrial ecosystems of the United States (Pardo et al. 2011).

Long-term experiments can provide a unique opportunity to directly evaluate the consequences of policy changes using an adaptive-management approach. In adaptive-management experiments, the researcher attempts to learn about managed systems by experimentally changing policy and assessing the outcomes on the appropriate time scale. At the NTL site, several policies were enacted as part of a long-term experiment designed to reduce P inputs and to control algal blooms in Lake Mendota, Wisconsin. Initial changes to land-use practices revealed little effect of management on the P inputs to the lake, possibly because of resuspension of P stored in sediments. Subsequent manipulation of the Lake Mendota food web to create a trophic cascade was more effective in reducing algal blooms, especially when they were accompanied by fishing-regulation changes and additional land-use practices implemented in the 1990s and 2000s (Carpenter et al. 2006).

Future policy can also be informed by results from long-term experiments. Work at the KBS site suggests that agricultural nitrous oxide (N\(_2\)O) emissions (figure 3) increase exponentially with increasing rates of N fertilizer use, after the rates exceed the N-uptake capacity of the crop. In intensive agricultural systems, application of N in excess of plant needs is rather common, because fertilizer is inexpensive relative to commodity prices, and producers tend to hedge against the risk of insufficient N in order to achieve maximum yields. Using the concept of maximum return to N, Millar and colleagues (2010) developed a transparent N\(_2\)O-reduction protocol suitable for incentivizing N\(_2\)O reductions without affecting crop yields. They estimated that if the protocol were widely adopted as a part of future C cap-and-trade markets, the protocol could reduce N\(_2\)O from fertilized row-crop agriculture by more than 50%.

Long-term experiments as platforms for new and unplanned research. Because of their multiyear nature, long-term experiments can serve as platforms for research that goes well beyond the goals originally envisioned. As a result, they provide opportunities for novel studies that take advantage of imposed treatments, as well as for more detailed process-level studies to uncover mechanisms behind long-term patterns. For example, the soil-warming studies at the HFR site have become a platform for new studies of soil C; the consequences of garlic mustard invasion, an exotic species that inhibits mycorrhizae and the growth of some tree seedlings; and for microbial studies of the mechanisms responsible for the pattern of increased heterotrophic soil respiration followed by a diminishing response to warming (Bradford et al. 2008). This latter research showed that the apparent acclimation of soil respiration at the ecosystem scale results from the combined effects of reductions in soil C pools and microbial biomass and changes in the thermal response of microbial respiration. Mass-specific respiration rates were lower when seasonal temperatures were higher, which suggests that rate reductions under experimental warming probably occurred through temperature-induced changes in the microbial community.

The long-term nutrient-addition studies that were conducted at multiple LTER sites to understand the role of N limitation, as well as to test ecosystem response to enhanced N deposition, have similarly provided a rich template for more short-term mechanistic studies. At the NWT site, for example, these studies have identified the importance of plant species traits in affecting community change (Suding et al. 2006) and demonstrated how plant–microbial feedbacks influence species coexistence (Ashton et al. 2008). Experiments initially designed to study vegetation change have been used to provide important insights as to how increased N availability can affect soil C storage (Neff et al. 2002).

Long-term experiments are increasingly serving as platforms for ecological metagenomics studies. At the SEV site, for example, microbial ecologists are examining the metagenomic responses of rhizosphere microbes in a fully crossed
multifactor experiment that includes increased winter rainfall, N amendment, and nighttime warming (Collins et al. 2010). At the CDR site, metagenomic studies have shown a marked divergence of microbial communities in grassland communities developed under ambient as opposed to elevated CO$_2$ in terms of both composition and function, with communities under elevated CO$_2$ exhibiting increased abundance of the genes involved in labile C decomposition and C and N fixation (He et al. 2010).

**A call for a new generation of long-term experiments**

We have argued that well-designed long-term experiments focused on key questions and important processes can have tremendous value for individual sites. These long-term experiments can provide the understanding necessary for forecasting, coping with, and mitigating the consequences of human-driven global changes to the environment (Collins et al. 2011). However, the scope and pace of change occurring in ecological systems today—and forecast for the future—are, by all accounts, unprecedented in human history (Palmer et al. 2004, Solomon et al. 2007, Smith et al. 2009). Because of the global scale of altered biogeochemical cycles from increased atmospheric CO$_2$ concentrations, nutrient enrichment and depletion, climatic change (means and extremes; Smith 2011), exotic species introductions, and land-use change, all ecosystems are, and will continue to be, affected by these alterations (Solomon et al. 2007). Independently conducted site-based studies in which global-change factors (i.e., N or temperature) were manipulated and modeling studies both show that responses to these global-change factors may vary dramatically among ecosystems—from little or no response to a substantial change in function (e.g., Weltzin et al. 2003). But experimental ecologists need to think beyond the site level and provide a more complete understanding of how and why ecosystems differ in their susceptibility and sensitivity to these changes. Such understanding is critical for forecasting the ecological consequences of global change at regional to continental spatial scales and yet it is a challenge that ecologists have not fully met (Smith et al. 2009).

This lack of comprehensive understanding occurs, in part, because ecologists have historically conducted disparate, largely independent experiments that tend to differ markedly with regard to (a) what is manipulated, (b) how much and for how long manipulations occur, and (c) what (and how) response variables are measured. This is certainly true of long-term experiments conducted in the LTER Network. As a result, syntheses across these studies can be difficult, since there is no way of knowing how much these different approaches contribute to the range of responses observed among ecosystems (Knapp et al. 2004). As Callahan (1984) pointed out more than 25 years ago, “even similar projects are not often comparable unless effort and resources have been devoted to making them so. This inherent tendency away from comparability becomes more prominent among projects conducted at locations that are geographically and biologically disjunct” (p. 363). Recently, renewed calls have been made for establishing unified sampling protocols and conducting simultaneous multisite, multifactor experiments to address the most pressing global-change issues (Janzen 2009, Luo et al. 2011; e.g., The Nutrient Network, http://nutnet.science.oregonstate.edu). We echo and extend these calls by proposing that these multisite experiments should be planned as long-term experiments capable of elucidating both ecological dynamics and ecological mechanisms. As is appropriate, these should take advantage of the long-term observations and contextual understanding extant within the LTER Network as well as from nonnetwork sites and other existing and emerging observatories (Carpenter 2008, Robertson et al. 2012 [in this issue]).

Designing multisite experiments will not be without challenges. For example, how one scales treatment levels across disparate ecosystems can influence how these different ecosystems respond to “common treatments.” For experiments that alter CO$_2$, treatments can be designed to increase CO$_2$ by either a constant amount or a constant proportion with an expectation of comparable results because essentially all terrestrial ecosystems have very similar atmospheric CO$_2$ concentrations. But for resources such as water and N, initial stocks and turnover rates can vary by orders of magnitude among mesic or xeric and fertile or infertile ecosystems. Therefore, experiments designed to increase or decrease resources by a constant proportion of availability and those designed to change them by a constant amount will likely lead to very different responses among sites. As was noted above, long-term data from observations and monitoring at LTER sites and the rich array of shorter-term process-level studies that each site has conducted can be invaluable for providing the appropriate context for planning such experiments, as well as for interpreting their results. Long-term data can also provide the breadth of understanding necessary for devising more-detailed studies that are often necessary for elucidating key mechanisms. Other issues that must be addressed, and that LTER scientists grapple with today, include determining the end point for long-term experiments (e.g., when do the costs outweigh the new knowledge gained by continuing an experiment?) and how to optimally balance the trade-off between the spatial scale of manipulations and the number of replicates. Small-plot-based long-term experiments, such as those at the CDR site, can be designed to be statistically robust with many replicates. This is not feasible with large-scale whole-watershed manipulations, such as those at the HBR site (figure 1). The scale of manipulations also determines the degree to which long-term experiments can serve as platforms for additional research. These are important tradeoffs in design that need to be considered for future long-term experiments.

We further advocate that such multisite long-term experiments should be designed in close collaboration with ecological modelers in order to alleviate the more vexing uncertainties in today’s models (Luo et al. 2011). Scenario planning (Peterson et al. 2003) can also be a valuable tool for designing experiments capable of providing information
relevant to stakeholders in addition to ecologists. These long-term experiments should be as large in scale as is feasible in order to permit the evaluation of ecological processes not possible in small-plot experiments (Smith et al. 2009). Designing large-scale experiments will present many unique challenges, since they are not simply big versions of the small-scale manipulations that ecologists have conducted in the past. Innovation in experimental design, statistical analysis, and engineering will be necessary. But as was noted above, with space set aside to accommodate unanticipated use, these networks of large-scale experiments would also serve as valuable research platforms for the broader ecological community. A highly coordinated and spatially extensive network of multifactor long-term experiments that adopts such a comparative approach would provide understanding and quantitative response data on ecological change at a temporal and spatial scale heretofore unavailable to ecologists. Such a network of experiments would complement the monitoring-based approach that the emerging National Ecological Observatory Network (NEON) has adopted by providing experimentally defined units of accelerated or amplified ecological change. Data from multisite, long-term experiments can be fused with models (Luo et al. 2011) to make more-robust forecasts for a broad range of ecosystems. Such forecasts can then be tested against the real-time tracking of ecological change provided by NEON and other observatory networks—and, of course, by the LTER Network.

For long-term experimental networks as they are envisioned above to be realized, it is clear that clever designs, collaborations between ecologists and sensor and infrastructure engineers (Collins et al. 2006), and efficient deployment will be necessary from both scientific and economic perspectives. But as society demands the knowledge needed to cope with and mitigate global changes, ecologists would be remiss in forgoing the opportunity to build on the legacy of long-term experiments reviewed above to meet these challenges.

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Ecosystem Processes and Human Influences Regulate Streamflow Response to Climate Change at Long-Term Ecological Research Sites


Analyses of long-term records at 35 headwater basins in the United States and Canada indicate that climate change effects on streamflow are not as clear as might be expected, perhaps because of ecosystem processes and human influences. Evapotranspiration was higher than was predicted by temperature in water-surplus ecosystems and lower than was predicted in water-deficit ecosystems. Streamflow was correlated with climate variability indices (e.g., the El Niño–Southern Oscillation, the Pacific Decadal Oscillation, the North Atlantic Oscillation), especially in seasons when vegetation influences are limited. Air temperature increased significantly at 17 of the 19 sites with 20- to 60-year records, but streamflow trends were directly related to climate trends (through changes in ice and snow) at only 7 sites. Past and present human and natural disturbance, vegetation succession, and human water use can mimic, exacerbate, counteract, or mask the effects of climate change on streamflow, even in reference basins. Long-term ecological research sites are ideal places to disentangle these processes.

Keywords: precipitation/runoff ratio, trend, succession, socioecological systems, Budyko curve

Although many factors affect streamflow, recent concerns have been focused on the effects of climate change on streamflow. Increasing temperature, more-severe storms, advanced snowmelt, and declining snow cover are associated with increased drought and flooding (Groisman et al. 2004, Stewart et al. 2005, Huntington 2006, Barnett et al. 2008, Karl et al. 2009, McDonald et al. 2011, USDOI 2011). Nevertheless, many human actions, natural disturbance effects, and ecosystem processes complicate, mitigate, and potentially counteract the climate effects on streamflow (Meybeck 2003, Jones 2011). Relevant human actions include ongoing disturbance and legacies of past disturbance, as well as global climate change. Understanding how climate change, social systems, and ecosystem processes affect streamflow is critical for mitigating conflicts between economic development and environmental conservation.

Long-term studies of headwater basins, the source areas for water supplies, provide an informative starting point for understanding the effects of climate, social factors, and ecosystem processes on streamflow (figure 1). The US Forest Service (USFS) Experimental Forests and Ranges (EFRs) and the US Department of Agriculture Agricultural Research Service (ARS) established long-term studies in small basins throughout the United States beginning in the early 1900s (see supplemental table S1, available online at http://dx.doi.org/10.1525/bio.2012.62.4.10). Four EFRs (AND, CWT, HBR, LUQ; for the site-name abbreviations, see table S1) and one ARS site (JRN) became member sites of the US Long Term Ecological Research (LTER) Network as early as 1980. Some LTER Network sites also utilize streamflow records from the US Geological Survey (USGS) National Water Information Service database. Some headwater basin studies participate in the USGS Hydrologic Benchmark Network; the USGS Water, Energy, and Biogeochemical Budgets (WEBB) program; or the Canadian HydroEcological Landscapes and Processes (HELP) program. Climate and hydrologic data from many sites have been publicly available since the 1990s (www.fsl.orst.edu/climhy).
Although they are less numerous than, for example, the USGS reference sites used in studies of climate change (e.g., Poff et al. 2007), LTER study sites provide unique insights into the interacting effects of social systems, ecosystems, and climate change on hydrology. In common with all ecosystems on Earth, the study basins have a long history of
natural disturbances and human impacts. Most of the study basins experienced no management during the period of record, but all of them are experiencing succession from past human disturbances; many continue to experience natural disturbances; and a few have agriculture, forestry, or residential development. Moreover, these study sites have matching records of climate drivers and hydrologic responses from (in most cases) relatively small areas. Therefore, these sites and analyses provide a unique opportunity to compare hydrologic responses to climate drivers over multiple decades and to interpret the responses on the basis of concurrent studies of social and ecosystem processes.

**A conceptual model of social systems, climate, ecosystems, and water**

The fundamental premise of the present article is that streamflow responds to ecosystem processes, which, in turn, respond both to climate drivers and to social drivers (figure 2). Social systems are a primary driver of streamflow through human water use and regulation and may indirectly affect streamflow through human-induced climate change. However, even in headwater ecosystems lacking human residents, social factors, including population dynamics, economic development, political conflicts, and resource policies, produce ecosystem disturbances, including forest harvest or clearance, grazing, agriculture, mining, and fire. In turn, these disturbances influence ecological succession, evapotranspiration, and streamflow.

Climate drivers—especially precipitation, temperature, snow and ice, and extreme events—also create ecosystem disturbances (e.g., wildfires, floods, wind and ice storms). Ecosystems continuously respond to disturbances (both human and natural) through ecological succession, and disturbances and responses differ among biomes. Ecosystems, social systems, and climate also respond to streamflow. Headwaters provide water for downstream ecosystems and communities, and ecosystem processes drive climate through evapotranspiration and energy exchange (figure 2).

Many of the study sites experienced social effects on ecosystem processes prior to becoming LTER sites. Most of the temperate forest in the eastern half of the United States and Canada and tropical forests in Puerto Rico experienced forest harvest, land clearance for agriculture, and grazing, followed by land abandonment (Swank and Crossley 1988, Foster and Aber 2004). Sites in the southwestern United States experienced intensive grazing of domestic animals during the past four centuries (Peters et al. 2006). Boreal forest, temperate wet forest, and tundra sites experienced varying fire regimes, mostly driven by climate but, in some cases, affected by prehistoric peoples (e.g., Weisberg and Swanson 2003). Some sites contain agriculture, forestry, and urban development.

In this study, we primarily examine the relationship between climate and streamflow on the basis of energy exchange. In cases in which streamflow behavior cannot be explained purely by climate, other hydrologic processes, as well as past and present human and natural disturbance effects on ecosystems, are considered as possible explanations.

**Study sites and questions**

In this study, we examined long-term records of air temperature (T), precipitation (P), and streamflow (Q) from 35 basins at US LTER Network sites, USFS EFRRs, USGS WEBB sites, and Canadian sites (table S1, figure 3a, 3b). The study sites were headwater basins that have mostly experienced no management since their records began. Nevertheless, the study basins have undergone succession in response to earlier natural or human disturbance, and some basins experienced natural disturbance during the periods of record. The records of T, P, and Q were obtained from the US LTER Network’s Climate and Hydrology Database Projects (ClimDB/HydroDB; http://climhhy.lternet.edu), supplemented by USGS streamflow data (http://co.water.usgs.gov/lochvate, http://ny.cfr.usgs.gov/hbn) and data from the Canadian HELP program (table S1).

The study basins ranged from 0.1 to 10,000 square kilometers; 2 were less than 10 hectares (ha); 5 were 10–100 ha; 10 were 100–1000 ha; 5 were 1000–10,000 ha; 8 were 10,000–100,000 ha; 2 were 100,000–1 million ha; and 2 were undefined (FCE, MCM; see table S1). The two largest basins were near ARC and GCE; eight additional large basins are located in the vicinity of CAP, HFR, JRN, KBS, NTL, OLY, PIE, and SEV. The smallest basins (smaller than 100 ha) are mostly associated with USFS or Canadian sites, at AND, BES, CWT, DOR, FER, HBR, MAR, and TLW.

The study sites represent many biomes (potential vegetation) (figure 4). More than half of the sites were temperate forest (CAS, CWT, DOR, HBR, HFR, FER, KEJ, MAR, MRM, NTL, PIE, TLW), temperate wet forest (AND, CAR, MAY, OLY), and boreal forest (ELA, FRA, LVW, TEN, UPC). The remainder includes tundra or cold desert (ARC, MCM, NWT), warm desert (CAP, JRN, SEV), cool desert or woodland (BNZ), woodland or grassland (BES, FCE, GCE, KBS, KNZ, SBC), and tropical rainforest (LUQ). Actual
Figure 3. (a) Map of sites used in this analysis. The study-site characteristics and abbreviations are in supplemental table S1, available online at http://dx.doi.org/10.1525/bio.2012.62.4.10. The symbols indicate which of the three analyses (Budyko curve, trends, and correlation with climate indices [oscillations]) were conducted with data from that site. (b) Map of average annual precipitation (P) minus potential evapotranspiration (PET) in millimeters (mm) with study-site locations.
and potential vegetation may differ because of disturbance (table S1).

In our analyses, we examined three questions, using successively more-stringent requirements of data sets and interpreted these results in the light of ecological and social factors: (1) How is potential evapotranspiration (PET) related to actual evapotranspiration (AET) at each site, and how do these relationships compare with the theoretical Budyko curve ($n = 30$ sites)? (2) How is streamflow correlated with climate indices (e.g., the El Niño–Southern Oscillation [ENSO], the Pacific Decadal Oscillation [PDO], the North Atlantic Oscillation [NAO]; $n = 21$ sites)? (3) How have temperature, precipitation, and streamflow changed over time ($n = 19$ sites)?

**Energy- and water-balance relationships to observed water use**

The values of $T$, $P$, and $Q$ from 30 sites with matched $T$, $P$, and $Q$ (table S1, figure 3) were used to calculate PET and AET (i.e., $P – Q$). These values were plotted on the Budyko curve (Budyko 1974), which displays the relationship between PET and AET, each indexed by $P$ (figure 5a). Thirty of the 35 sites had data on $T$, $P$, $Q$, and basin area for a common 10-year period (1993–2002), although a slightly adjusted period was used for 10 of the sites (figure 5b). PET was calculated from $T$ (after Hamon 1963) on the basis of the number of daylight hours, mean monthly temperature, and the saturated vapor pressure. Annual PET was calculated as a sum of monthly values. The Budyko curve assumes that the water balance is $Q = P – ET$ (evapotranspiration), with no significant losses to or gains from groundwater, and that the basins are at steady state, unaffected by vegetation dynamics (Donohue et al. 2007).

The distribution of study basins on the Budyko curve reveals that observed water use in ecosystems in small basins deviated systematically from its expected dependence on energy and water balances. As was expected, observed ecosystem water use ($AET + P$) was positively correlated to energy and water inputs to evapotranspiration ($PET + P$) in sites with a water surplus ($P > PET$) and insensitive to increases in energy at sites with a water deficit ($P < PET$), following the theoretical Budyko curve (figure 5b). However, only 7 of 30 sites (ARC, DOR, FRA, HBR, KEJ, KNZ, and OLY) fell on the Budyko curve, where observed water use ($AET + P$) was equal to predicted water use ($PET + P$) (figure 5b). Of the 19 sites with a moisture surplus ($P > PET$) that did not fall on the Budyko curve, 14 were above it, with higher than expected evapotranspiration ($AET + P > PET + P$). Of the five sites with moisture deficits ($P < PET$), four fell below the Budyko curve, with lower than expected evapotranspiration ($AET + P < PET + P$) (figure 5b).

This result may indicate that ecosystems evaporate, transpire, and store more water than would be expected on the basis of temperature and day length at wet sites and less than would be expected at dry sites. Ecosystem structure (e.g., rooting depth, leaf area) and processes (e.g., adaptations to water deficits) may produce lower streamflow in wet sites and higher streamflow in dry sites than would be predicted from energy and water balances alone. However, other factors may also explain the departures of the sites from the theoretical Budyko curve. For instance, the PET value estimated from climate-station $T$ records may not represent PET over entire basins, especially in mountain sites (e.g., AND, NWT, LVW). AET + $P$ is also considerably overestimated from $P – Q$ in basins in which the groundwater recharge bypasses the stream gauge (Graham et al. 2010, Verry et al. 2011).

When the annual values of $T$, $P$, and $Q$ are plotted on the Budyko curve, the interannual variation of AET relative to PET varies among biomes (figure 5c, 5d). Variation in $AET + P$ was less than in $PET + P$ at the desert sites (CAP, SEV) and at forested sites (AND, CAS, CWT, FER, HBR, MAR, NTL) (figure 5d). In contrast, at alpine sites (LVW, NWT), the interannual variation in AET + $P$ was large relative to the variation in $PET + P$. This behavior of sites relative to the Budyko curve implies that ecosystems are capable of adjusting AET to compensate for climate variability at desert, grassland, and forest sites, but less so at alpine sites.

Ecosystems have more-similar rates of net primary productivity per unit precipitation in dry than in wet years (Huxman et al. 2004). Comparisons of long-term AET and PET from study basins to the theoretical Budyko curve (figure 5) suggest that AET varies in a narrower range than would be expected from energy and water balances alone, which underscores the importance of ecosystem process effects on streamflow.
Streams and regional climate oscillations

We examined the relationship of three climate indices (ENSO, PDO, and NAO) to Q at 21 sites (tables S1 and S2). These indices measure multyear or multidecadal oscillations of sea-surface temperatures and atmospheric-pressure differentials in the east–central tropical Pacific (ENSO), the northern Pacific (PDO), and the northern Atlantic (NAO). They are correlated with local and regional temperature, precipitation, and streamflow in the United States (Cayan et al. 1999, Barlow et al. 2001, Enfield et al. 2001). The sites included in this analysis had fewer than 10 years of continuous (monthly) Q at one or more gauging stations, separated into a cool season (November–April) and a warm season (May–October). Correlated streamflow records (Pearson’s r > .80) were pooled at study sites with multiple stream gauges. Climate indices were obtained from online databases (NAO, www.cgd.ucar.edu/cas/jhurrell/indices.html; ENSO, www.cdc.noaa.gov/ClimateIndices/List; PDO, www.esrl.noaa.gov/psd/data/correlation/pdo.data). The streamflow–climate oscillation relationships were tested using generalized least squares models with autoregressive moving average functions; the models were evaluated with the Durbin–Watson test statistic and Akaike’s information criterion. The results are shown as the sign (+ or –) of the relationship of streamflow to each index at each site.
to climate oscillation variables that were significant at $\alpha < .10$ in the models (table S2).

The cool-season (November–April) and warm-season (May–October) streamflow values were significantly correlated with at least one climate index or interaction term at all sites except FRA, KNZ, NWT, and PIE (table S2). Significant correlations of streamflow were more frequent with ENSO (11, plus six interactions) and PDO (10, plus one interaction) than with NAO (4, plus six interactions) (table S2). Significant correlations were also slightly more frequent in winter (18) than in summer (14). These findings extend Greenland and colleagues’ (2003) analysis of climate indices, temperature, and precipitation at US LTER Network sites and corroborate the results of other studies. Molles and Dahm (1990) noted that streamflow in two rivers in New Mexico was significantly higher during El Niño (warm sea-surface temperatures in the eastern Pacific) than during La Niña conditions. Cayan and colleagues (1999) showed that days with high daily precipitation and streamflow were more frequent than average in the US Southwest and less frequent in the Northwest during El Niño by examining effects on snowpack accumulation and the subsequent melt. Enfield and colleagues (2001) found that sea-surface temperatures in the northern Atlantic are correlated with those in the northern Pacific and are associated with variations in streamflow in the Mississippi River and in Florida. Sea-surface temperature and pressure anomalies originating in the North Pacific affect cyclonic circulation over the East Coast and summer precipitation, streamflow, and drought (Barlow et al. 2001).

These findings underscore the importance of separating the effects on streamflow of climate variability from long-term trends. Because the ENSO oscillation has a wavelength of 2–7 years, trends in climate and streamflow data sets over fewer than 20 years may simply reflect ENSO. Similarly, the PDO has a wavelength of 4–16 years (MacDonald et al. 2005), with mostly negative PDO in the 1950s to the mid-1970s and mostly positive PDO from 1976 to 1998. The NAO was predominantly negative between the 1950s and the early 1970s and was mostly positive between the 1980s and the early 1990s. As a result, climate and streamflow trends from the 1950s to 2000 may be strongly affected by these climate oscillations. For example, at ARC, streamflow increased between 1988 and 2003, but declined between 1988 and 2008, so lengthening the record shifted the direction of apparent change. The lack of statistically significant increases in minimum temperature at the tundra ARC and boreal forest LVW sites (see the next section) may also be attributed to confounding effects of climate oscillations on these relatively short-term records.

Climate oscillations influence ecosystem processes through streamflow and moisture. Streamflow was slightly more weakly correlated to climate indices in summer than in winter, perhaps because precipitation and streamflow are more closely related when ecosystems are dormant. ENSO is linked to aquatic-community structure in the Southwest (Sponseller et al. 2010), PDO is related to salmon returns in the Northwest (Mantua et al. 1997), and NAO is linked to stream salamander abundance in the Southeast (Warren and Bradford 2010). Headwater streamflow records are just beginning to be long enough to relate climate variability and trends to ecosystem processes and population dynamics.

**Climate and streamflow trends at long-term headwater basin study sites**

Nineteen sites had long-term records suitable for testing trends in T, P, and Q (table S1). Sites were included in the analysis if they had overlapping records of T, P, and Q that exceeded 20 years. The climate and streamflow record lengths used for trend estimation ranged from 20 to just over 60 years; five were 20–30 years; one was 30–40 years; four were 40–50 years; seven were 50–60 years; and two were more than 60 years (table S1). The records exceeding 40 years are from USGS gauges and nearby climate stations (CAP, GCE, JRN, OLY, SBC, SEV), USFS EFRs that became US LTER Network sites (AND, CWT, HBR), other LTER Network sites (HFR), and USFS EFRs (FER, MAR) that did not become LTER Network sites. The records less than 40 years in length were USGS gauges and nearby climate stations at LTER Network sites, WEBB sites, and EFRs (ARC, FRA, LUQ, LVW, NTL, and NWT).

Interannual trends in minimum and maximum daily T, P, Q, and runoff ratios (Q:P) were estimated using linear regression and the Mann–Kendall nonparametric trend test (Helsel and Hirsch 2002). In these analyses, we used the period of record or from 1950 onward. Linear regressions and Mann–Kendall tests produced almost identical results (Hatcher 2011). The water year was defined as 1 October to 30 September. Tests were conducted using daily data. The daily P and Q values were log transformed before analysis. Data were tested for autocorrelation before analysis, and residuals from linear regression analyses were also tested for autocorrelation. Significant trends in annual T, P, and Q were defined as 10 or more days (out of 365) with significant trends (at $\alpha \leq .025$) and no autocorrelation before regression or in the residuals, and an average slope of the trend in daily values exceeding its standard error.

Annual minimum or maximum daily temperature increased significantly at 17 of the 19 sites (minimum temperatures increased at 13 sites and maximum temperatures increased at 7 sites), but only two sites experienced significant changes in precipitation over the period of available record (figure 6). Minimum daily temperatures increased by several degrees Celsius since 1980 at NWT and FRA, high-elevation, snow-dominated sites in the Rocky Mountains, but not at the other high-elevation Rocky Mountain site (LVW). Minimum daily temperature also increased by several degrees Celsius since the 1950s at climate stations near JRN and SEV in New Mexico, since the 1950s at a southeastern temperate forest site (CWT), and since the 1960s at a northern hardwood site (MAR) but not at its neighbor...
Streamflow changes vary according to the season and differ among various biomes (figure 7). At undisturbed desert sites in Arizona (CAP) and New Mexico (SEV), streamflow did not change at any time of year (figure 7a, 7b). However, in a desert mountain basin northeast of JRN (New Mexico) and in a semiarid mountain basin near SBC (southern California) containing residential and urban development, streamflow increased during low-flow periods (figure 7c, 7d). In a large basin in coastal Georgia containing agriculture and forest plantations (GCE), streamflow declined in early and late summer (figure 7e).

At tundra sites on the North Slope of Alaska and in the Rocky Mountains (ARC, NWT; figure 7f, 7g), streamflow increased in early spring and late fall, during time periods adjacent to freezing periods. Streamflow increased in spring at boreal forest sites in the Rocky Mountains (FRA, LVW; figure 7h, 7i). At a temperate forest site in western North Carolina (CWT), where seasonal snowpacks do not form, streamflow did not change at any time of year (figure 7j), but at a temperate forest site in West Virginia (FER), streamflow did not change at most other sites, which mostly lack significant snow and ice (Hatcher 2011).

Runoff ratios (Q:P) changed at 8 of 19 sites (figure 6b). Tundra and boreal forest sites with ice and permafrost (LVW, NWT) experienced increases in runoff ratios, and so did temperate deciduous forest sites in the northeastern United States (HBR, HFR, PIE), which have a seasonal snowpack. An increase in runoff ratio means either that AET has decreased, or that there is a net addition of water to the system, such as from melting ice or interbasin water transfers. The observed increases in runoff ratios at LVW and NWT may be associated with the melt of ice, snow, and permafrost in response to warming temperatures during seasons in which these ecosystems are dormant (not taking up water). However, warming did not result in increased runoff ratios at other sites with permafrost (ARC, which has a short record) or seasonal snowpacks (e.g., AND, FRA, MAR, NTL). Runoff ratios did not change at most other sites, which mostly lack significant snow and ice (Hatcher 2011).
Figure 7. Daily changes in streamflow at 19 US Long Term Ecological Research sites, US Forest Service Experimental Forests and Ranges, and US Geological Survey Water, Energy, and Biogeochemical Budgets sites arranged by biome (from figure 4) as a function of the day of the water year (1 October to 30 September). (a–c) Desert sites (CAP, SEV, JRN); (d), (e) savanna sites (SBC, GCE); (f), (g) tundra sites (ARC, NWT); (h), (i) boreal forest sites (FRA, LVW); (j–p) temperate forest sites (CWT, FER, HFR, HBR, MAR, NTL, PIE); (q), (r) wet temperate forest sites (AND, OLY); (s) wet tropical forest site (LUQ). The vertical axis and the green line are the slope of regression of log-transformed streamflow for each day of the water year over the period of record (see supplemental table S1, available online at http://dx.doi.org/10.1525/bio.2012.62.4.10). The vertical axis units are the proportion change per year relative to the mean daily flow. The percentage change can be calculated as $(1 + p)^n$, where $p$ is the proportion change and $n$ is the number of years. Note the different vertical axis scales. The horizontal black line represents no change (a proportion change of 0); the wiggly black lines are the upper and lower bounds on the 97.5% confidence interval. The red dots represent significant increases, and the blue dots represent significant decreases in daily streamflow, where $\alpha \leq .025$. 

\[ \text{Proportion change per year relative to the mean daily flow} \]

\[ \text{Month} \]

\[ \text{CAP – Sycamore Creek – 1961–2010} \]

\[ \text{SEV – Jemez River – 1954–2010} \]

\[ \text{JRN – Rio Ruidoso – 1950–2010} \]

\[ \text{SBC – San Jose Creek – 1950–2010} \]

\[ \text{GCE – Ochooppee River – 1950–2009} \]

\[ \text{ARC – Kuparuk River – 1971–2010} \]

\[ \text{NWT – Green Lake 4 – 1981–2008} \]

\[ \text{FRA – East Saint Louis – 1976–2005} \]

\[ \text{LVW – Loch Vale outlet – 1984–2010} \]

\[ \text{CWT – WS18 – 1950–2009} \]
increased in the summer (figure 7k). Winter streamflow increased at three temperate forest sites in New England (HFR, HBR, PIE) and declined at one (NTL) (figure 7l, 7m, 7o, 7p). In addition, streamflow increased in March and decreased in April at HBR (figure 7m), and it increased in March and declined in summer at MAR (figure 7n). At wet temperate forest sites in Oregon (AND, OLY), streamflow declined in spring (figure 7q, 7r). Streamflow did not change at any time of year at a wet tropical forest site in Puerto Rico (LUQ) (figure 7s).

**Figure 7. (Continued)**

Social, ecological, and climate factors influencing streamflow trends
Multiple social and ecological factors may explain the streamflow trends at long-term headwater basin sites, even though humans do not directly affect most of these sites (figure 2). Economic development, population growth, and the use of fossil-fuel resources have increased atmospheric carbon dioxide, warmed the Earth, contributed to more-intense precipitation events, and increased evapotranspiration...
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(Min et al. 2011, Pall et al. 2011), which in turn have been linked to increased flooding and drought (Barnett et al. 2008, Karl et al. 2009). Yet direct climate-trend effects on streamflow in headwater basins may be mitigated by ecological processes, including disturbance, succession, and vegetation adaptations to water scarcity. In many cases, the vegetation—and, therefore, evapotranspiration in headwater basins—is affected by human activities, such as past logging, grazing, agriculture, and fire suppression. Moreover, in some headwater basins, land-use changes, including agriculture and exurban expansion, may mitigate or overwhelm climate-trend effects on streamflow.

Some observed trends in streamflow appear to be direct effects of climate trends. For example, increased streamflow in fall and spring at ARC, FRA, and NWT is probably the result of the expanding period of thaw at these tundra and boreal forest sites (figure 7f, 7g, 7i). Increases in streamflow at these sites may be driven by permafrost melt; changes in the chemical composition of streamflow support this hypothesis (Bowden et al. 2008, Caine 2010). In addition, increased spring streamflow at temperate forest sites with seasonal snowpacks in New England (HBR) and in the upper Midwest (MAR) is probably the result of earlier snowmelt, whereas increased winter streamflow at temperate forest sites in New England (HFR) may be the result of a shift from snow to rain. These responses are consistent with the results of published studies (Hodgkins et al. 2003, Stewart et al. 2005, Clow 2010, Campbell et al. 2011).

Some observed trends in streamflow may be the result of biological responses to climate change. For example, declining streamflow at a woodland site (summer at GCE), a boreal forest site (LVW), temperate forest sites (MAR, NTL), and wet temperate forest sites (spring at AND, OLY) may be the result of increased evapotranspiration in response to warmer temperatures. Conifer forests, which occur at MAR, NTL, LVW, AND, and OLY, are adapted to photosynthesize and respire when conditions are favorable; warmer temperatures may lead to an earlier onset of transpiration and to declining streamflow (e.g., Moore KM 2010). Streamflow trends at wet temperate and boreal forest sites (LVW, AND, OLY; figure 7) are restricted to the immediate period of snowmelt, and declines may reflect increased evapotranspiration (Moore KM 2010, Oishi et al. 2010, Campbell et al. 2011). In contrast, streamflow trends are largest during the nonsnowmelt periods at temperate forest sites in the upper Midwest (NTL, MAR), where wetlands (bogs and lakes) occupy a large proportion of basin area (Verry et al. 2011). Increased evapotranspiration associated with declining ice cover (Magnarson et al. 2000) or increased radiation associated with decreased precipitation may account for declining flows at these sites.

Some sites experienced no trends in streamflow, despite increases in temperature. For example, desert sites (CAP and SEV) and the wet tropical site (LUQ) experienced significant increases in minimum and maximum daily temperatures, no change in precipitation (figure 6), and almost no changes in streamflow (figure 7a, 7b, 7s). Vegetation adaptations to drought might explain the lack of a streamflow response to warming at the desert sites. At the wet tropical forest site, the effects of the 1996 Hurricane Hugo on leaf area, evapotranspiration, and streamflow (Scatena et al. 1996) may have overwhelmed climate-trend effects.

Some sites experienced trends in streamflow that appear to be biological responses to past disturbances. For example, forest succession and declining evapotranspiration may explain increased summer streamflow at two temperate forest sites (FER, HBR), which were logged in the early nineteenth century (figure 7k, 7m). At a third temperate forest site (CWT), streamflow and runoff ratios have not changed, despite increases in air temperature (figure 6, figure 7j). Forest succession following disturbances in the early 1900s at all three sites (table S1; Swank et al. 2001, Adams et al. 2006) and associated changes in species composition or leaf area may have influenced streamflow trends. Analyses of long-term paired-basin experiment data (e.g., Jones and Post 2004) indicate that streamflow continues to change over decades or centuries of forest succession after disturbance.

Responses to land use and disturbance, such as advanced snowmelt or declining summer streamflow, may be misconstrued as responses to climate change. In paired-basin experiments (see the discussion of long-term experiments in Knapp and colleagues 2012 [in this issue]), forest harvest advanced the timing of peak snowmelt and associated streamflow by up to three weeks in temperate forest sites with a seasonal snowpack (AND, HBR); the effect lasted for more than 10 years (Jones and Post 2004). By 25 to 35 years after forest harvest in temperate forest basins (AND, CWT, HBR), summer streamflow declined by up to 30%–50% relative to the reference basins (Hornbeck et al. 1997, Swank et al. 2001, Jones and Post 2004). Regenerating species in early forest succession may transpire more water per unit of leaf area and, in some cases, have greater total leaf area than the species that were removed, which would reduce summer streamflow (Swank et al. 2001, Moore GM et al. 2004).

Historic legacies from past disturbance in these long-term studies demonstrate that streamflow and timing responses to forest disturbance are at least as large as responses associated with climate trends over the past 20–60 years at the study sites. Daily streamflow during the late summer and early fall increased by up to 300% in the 1–5-year period after experimental forest harvest (AND, CWT, HBR), but most daily changes were on the order of 50% or less (Jones and Post 2004). By comparison, trends in daily streamflow associated with climate trends at the 19 study sites were on the order of 0.005–0.05 of log(Q) per year. The lower value is equivalent to changes of 10%–25%, and the higher value is equivalent to more than a 100% change over 20–60 years, but changes of this magnitude are restricted to a few days per year (figure 7).

Finally, some observed trends in streamflow may be direct human effects on the hydrologic cycle. For example,
increased irrigation using groundwater or water imported from other basins may explain increasing streamflow during dry seasons at a desert site in New Mexico (JRN) and a savanna site in southern California (SBC), which have some agriculture and residential development (figure 7c, 7d). Increasing winter streamflow trends at a temperate forest site (PIE) may reflect urban expansion (Claessens et al. 2006). Therefore, human effects on streamflow may mimic, exacerbate, counteract, or mask climate effects on streamflow, making it challenging to determine the vulnerability of human communities (sensu Polsky et al. 2007) to variations in water supply.

Headwater basins in this study drain into major river systems that supply water to major agricultural areas and medium and large cities. Climate change is expected to increase the variability of future streamflow and to stress municipal water supplies (Milly et al. 2008, Covich 2010, McDonald et al. 2011, USDOI 2011). Long-term studies of headwater basins can help distinguish biophysical from social causes of variability in water supply and, hence, the relationships between ecological and social resilience (Adger 2000). Water scarcity may be perceived even in areas with abundant rainfall, where politics rather than true scarcity may govern water restrictions (Hill and Polsky 2006). Meanwhile, residents, professional policymakers, and academics in Phoenix (CAP) implicated population growth, climate change, and drought as the most important causes of water scarcity, rather than their own water-use habits (Larson et al. 2009). Adding to this research, in this study, we suggest that rather complex interactions among historical social factors, ecosystem processes, and climate influence the long-term water supply from headwater basins.

**The role of information management**

Long-term ecological data are critical to answering societal questions of national concern and significance. Long-term data are the only way to distinguish trends from short-term variability in key environmental indicators, such as climate and streamflow. However, many long-term data remain inaccessible or difficult to access. Many valuable data sets are stored in inconvenient file formats with limited metadata. Variations in methods, variables, units, measurement scales, and quality-control annotation complicate data integration and prevent automated approaches to data synthesis.

Until the 1990s, the difficulty of identifying, accessing, and integrating climate and hydrologic data from the LTER Network, EFRs, and related networks precluded cross-site studies. ClimDB/HydroDB (http://climhy.lternet.edu), a collaborative effort between LTER Network and USFS information managers, was initiated in 1997 to overcome these limitations. ClimDB/HydroDB is a Web harvester and data warehouse that provides uniform access and visualization of daily streamflow and meteorological data through a single portal. Participating sites manage original data within their local information systems but periodically contribute data to the warehouse. Although the ClimDB/HydroDB approach is not a complete solution to data-access and -integration issues, it has served as an effective bridge technology between older, more rigid data-distribution models and modern service-oriented architectures (Henshaw et al. 2006).

The LTER Network has made great strides in collecting, archiving, and integrating long-term data sets online, enabling synthesis activities such as this one, and providing an example for other environmental observatories. Information managers at LTER Network sites have led the development of metadata standards, data dictionaries, and software for data integration. The LTER Network data-management system serves as a model for emerging national observatories and existing programs.

**Conclusions**

This study provides an example of the special kinds of science that are possible from networks of long-term study sites. Climate and streamflow records are sufficiently long that averages, variability, and trends can be meaningfully analyzed. The climate and streamflow properties are simple and comparable because they are consistently measured across sites. Climate and streamflow data are broadly relevant to ecosystem processes and ecosystem services. Above all, multisite synthesis is fostered by and contributes to an open, inclusive culture of science collaboration.

This study showed that actual evapotranspiration was predicted by PET at only 7 of 30 sites with 10-year-long records (the Budyko curve). Taken individually, these departures might simply reflect the inability of a climate station to represent the conditions of a whole basin or the fact that streamflow depends on groundwater and other forms of storage, as well as precipitation and temperature. But taken collectively, the departures of these sites from the Budyko prediction suggest the intriguing hypothesis that water-scarce ecosystems evapotranspire less and water-abundant ecosystems evapotranspire more than would be predicted from their climates. Moreover, streamflow at many of these sites was significantly related to one or more climate index (ENSO, NAO, or PDO), which is not surprising, but the slightly more frequent significant correlations of streamflow with climate indices in winter than in summer imply that ecosystem processes mediate climate-streamflow coupling. Finally, 17 of 19 sites had significant increases in their minimum or maximum daily temperatures or both, but streamflow trends were directly related to climate trends at only 7 of the sites, all of which have permanent or seasonal ice and snow. In contrast, at other sites, and during certain seasons at these seven sites, streamflow trends were contrary to those expected from climate drivers.

A key finding from this study is that the past and present human uses of ecosystems and human water-use practices can mimic, exacerbate, counteract, or mask the effects of climate change on streamflow. Social factors, including
past land management and disturbance and the resulting ecological succession, all influence trends in streamflow, even at sites that are considered to be “reference” basins. In other words, exogenous (climate) factors are not the only drivers of nonstationarity (e.g., Milly et al. 2008) in streamflow from headwaters: Ecosystem processes and their social drivers are also important controls. In order to understand reference conditions for natural flow regimes (e.g., Poff et al. 2007), we need to better understand how ecological processes and social drivers mediate the expression of climate on streamflow. Long-term study sites, where all these processes are being studied, are ideal places for this ongoing work.

Acknowledgments
Funding for this work was provided by the US Long Term Ecological Research (LTER) Network and National Science Foundation grants to participating sites and by a Natural Sciences and Engineering Research Council of Canada Discovery Grant to IFC. We thank LTER Network information managers for the creation and maintenance of ClimDB/HydroDB; the US Forest Service for the initial establishment and continued support of climate and basin measurements at many of the study sites; the US Geological Survey (USGS) Water, Energy, and Biogeochemical Budgets program, the USGS Hydrologic Benchmark Network, and the USGS National Water Information Service for provision of data; and the Networks of Centres of Excellence–Sustainable Forest Management Network–funded project on HydroEcological Landscapes and Processes (HELP) and the participating Canadian experimental basins from which data were contributed to the HELP project (Peter Tschaplinski for CAR, Tom Clair for KEJ, Fred Beall for TLW and MRM, Ray Hesslein for ELA, Peter Dillon for DOR, and Rita Winkler for UPC). We thank Merryl Albers, David R. Foster, Eveleyn Gaiser, Ann Giblin, Stephen P. Loheide II, Randy K. Kolka, Richard V. Pouyat, Sylvia Schaefer, Emily H. Stanley, Frederick J. Swanson, Will Wollheim, and three anonymous reviewers for comments on the manuscript.

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The Disappearing Cryosphere: Impacts and Ecosystem Responses to Rapid Cryosphere Loss

ANDREW G. FOUNTAIN, JOHN L. CAMPBELL, EDWARD A. G. SCHUUR, SHARON E. STAMMERJOHN, MARK W. WILLIAMS, AND HUGH W. DUCKLOW

The cryosphere—the portion of the Earth's surface where water is in solid form for at least one month of the year—has been shrinking in response to climate warming. The extents of sea ice, snow, and glaciers, for example, have been decreasing. In response, the ecosystems within the cryosphere and those that depend on the cryosphere have been changing. We identify two principal aspects of ecosystem-level responses to cryosphere loss: (1) trophodynamic alterations resulting from the loss of habitat and species loss or replacement and (2) changes in the rates and mechanisms of biogeochemical storage and cycling of carbon and nutrients, caused by changes in physical forcings or ecological community functioning. These changes affect biota in positive or negative ways, depending on how they interact with the cryosphere. The important outcome, however, is the change and the response the human social system (infrastructure, food, water, recreation) will have to that change.

Keywords: cryosphere, ecosystem response, environmental observatories

Global average air temperature has warmed by 1 degree Celsius (°C) over the past century, and in response, the cryosphere—the part of the Earth's surface most influenced by ice and snow—is changing. Specifically, alpine glaciers are retreating, the expanse of Arctic sea ice has been shrinking, the thickness and duration of winter snowpacks are diminishing, permafrost has been melting, and the ice cover on lakes and rivers has been appearing later in the year and melting out earlier. Although these changes are relatively well documented, the ecological responses and long-term consequences that they initiate are not. Detailed studies have identified specific responses to individual components cryospheric changes (e.g., polar bear habitat and sea ice loss), but a more integrated view across many landscapes and types of changes has been lacking. In the present article, we draw largely—but not exclusively—from sites of the US Long Term Ecological Research (LTER) Network (the special section in this issue; see especially Robertson et al. 2012) to synthesize our current knowledge of ecosystem responses to the changing cryosphere in an attempt to infer broad responses and to anticipate the further range of changes that we might expect. We contend that place-based, long-term, interdisciplinary efforts, such as LTER-type projects, are the best suited for tracking such changes and for detecting and understanding their cascading effects throughout the ecosystem.

The cryosphere

For the purposes of this synthesis, the spatial extent of the cryosphere for the Northern Hemisphere includes the mean February extent of snow cover (measured between 1987 and 2003) and the mean March extent of sea ice (measured between 1979 and 2003). For the Southern Hemisphere, we include the mean August and September extents of snow and sea ice, respectively. Broad statistics for the cryosphere and its changes are provided in table 1 and are depicted in figure 1.

Permafrost (figure 2a) is widespread in the Arctic and boreal regions of the Northern Hemisphere, with the permafrost zone occupying about 24% of the exposed land area. Most of this (78%) occurs in lowlands below 1000 meters (m) of elevation, whereas deposits of alpine permafrost are widely distributed. Changes in permafrost are typically documented by two metrics: temperature and the depth to the permafrost, which is defined as the active layer, which in turn is the surface layer that thaws seasonally. Since the 1980s, permafrost temperatures have generally increased between 0.5° and 2°C when measured at about 10 m, a depth at which seasonal variations cancel each other out and thus yield a seasonally constant value (Romanovsky et al. 2007). At some Russian sites, where many data are available, the active layer increased by 1.7–5.5 centimeters (cm) per year over the 10-year period between 1997 and 2007.
(Mazhitova et al. 2008), whereas other sites have shown little change (Zamolodchikov et al. 2008). However, recent data have shown that active-layer depth measurements alone may obscure the degradation of permafrost, because the ground surface subsides as permafrost thaws and internal ice melts. This subsidence process (called thermokarst) can radically restructure surface hydrology by altering the dynamics of water bodies, initiating or expanding surface channel incision, and drying surface soil layers. Observations near Toolik Lake, Alaska, have shown rapid mass wasting of surface soils undergoing thaw, which resulted in an increased loading of suspended sediment in streams, with direct and indirect effects on stream biota (Bowden et al. 2008). In the McMurdo Dry Valleys of Antarctica, enhanced incision of stream water into massive subsurface ice has caused one river to flow underground for some distance. At Niwot Ridge in Colorado, increasing water flow and solute concentrations in early autumn have been attributed to the melting of alpine permafrost (Caine 2010).

One iconic and highly conspicuous feature of global warming is glacier recession (figure 2b).

Table 1. Components of the global cryosphere and their areal extent.

<table>
<thead>
<tr>
<th>Component</th>
<th>Definition and remarks</th>
<th>Extent (in $10^6$ km$^2$)</th>
<th>LTER site(s)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snow</td>
<td>Perennial or seasonal cover of the land surface: 98% in Northern hemisphere</td>
<td>1.9 (summer) 45 (winter)</td>
<td>ARC, AND, BNZ, CDR, KBS, KNZ, HBR, HFR, MCM, NTL, NWT, SGS, PIE,</td>
</tr>
<tr>
<td>Glaciers</td>
<td>Perennial snow or ice that moves Alpine glaciers and ice caps</td>
<td>0.53</td>
<td>MCM, NWT, PAL</td>
</tr>
<tr>
<td>Ice sheets</td>
<td>Subsurface Earth material remaining below 0 degrees Celsius for at least 2 years</td>
<td>14</td>
<td>MCM, PAL</td>
</tr>
<tr>
<td>Permafrost</td>
<td>Subsurface Earth material remaining below 0 degrees Celsius for at least 2 years</td>
<td>23</td>
<td>ARC, BNZ, MCM, NWT</td>
</tr>
<tr>
<td>Lake and river ice</td>
<td>Seasonal cover of lakes and rivers</td>
<td>?</td>
<td>ARC, AND, BNZ, CDR, KBS, KNZ, HBR, HFR, MCM, NTL, NWT, SGS, PIE</td>
</tr>
<tr>
<td>Sea ice</td>
<td>Perennial or seasonal cover of the ocean</td>
<td>19–27</td>
<td>PAL</td>
</tr>
</tbody>
</table>

Note: All extents are from table 4.1 of Solomon and colleagues (2007). The value for permafrost is the region in which permafrost occurs and includes both frozen and unfrozen soils. km$^2$, square kilometers; LTER, long-term ecological research.

*See table 2 for the site abbreviations.

Figure 1. Approximate geographic limits of the cryosphere. (a) January climatology of Northern Hemisphere sea ice (measured between 1979 and 2005) and snow extent (measured between 1967 and 2005) with the North Pole referenced (the red dot). (b) September climatology of Southern Hemisphere sea ice (measured between 1979 and 2003) and snow extent (measured between 1987 and 2002) with the South Pole referenced (the red dot). Source: Reprinted from John Maurer, Atlas of the Cryosphere. National Snow and Ice Data Center (2007; http://nsidc.org/data/atlas).
Glaciers have been receding worldwide since the end of the Little Ice Age in the late 1800s, although regional and temporal variations in recession have occurred (Dyurgerov and Meier 2000). In recent decades, glacier-mass loss has accelerated, with the increased rate ascribed to increased temperatures. Glacier change in the United States reflects these global trends through area losses over the past century of 34%–56% in the Sierra Nevada and the Cascades of Oregon and Washington and about 40% at Niwot Ridge, in the Colorado Front Range. In contrast to these observations and to those elsewhere in the alpine Southern Hemisphere, glaciers in the McMurdo Dry Valleys of Antarctica appear to be in equilibrium, since their positions have not changed since their observation began in 1993 (Fountain et al. 2006). The removal of water from long-term storage in glacial ice increases summer streamflow and global sea level. However, as the mass of glaciers decline, their ability to support summer streamflow declines, and they decrease in their ability to buffer the watersheds against drought.

Sea ice (figure 2c) occurs in the Arctic; in the Southern Ocean surrounding Antarctica and the Baltic Sea; and in part of the northwest Pacific, from the Siberian coast down to the Japanese island of Hokkaido. Most sea ice forms and melts annually, with perennial multiyear ice restricted to the high latitudes of the Arctic and Antarctica. Since the advent of continuous satellite monitoring in the late

Figure 2. Examples of the cryosphere. (a) Winter eastern forest, Mount Washington, New Hampshire (Photograph: Jerry and Marcy Monkman, www.ecophotography.com); (b) Melting sea ice and an iceberg, Charcot Island, Antarctic Peninsula (Photograph: Grace K. Saba, Rutgers University); (c) Massive ice exposed by degrading permafrost, Noatak National Preserve, Arkansas (Photograph: Edward A. G. Schuur); (d) Dana Glacier, Sierra Nevada, California. The top panel is the glacier in 1883 (Photograph: I. C. Russell, US Geological Survey); the bottom panel is from 2004 (Photograph: Hassan Basagic).
1970s, widespread decreases in sea ice have been recorded throughout most of the Arctic at an average rate of 3% loss per decade (Comiso and Nishio 2008). In contrast, decreases in Antarctic sea ice have been regionally confined and juxtaposed against regions of increasing sea ice, such that the average rate of change overall is a slight increase of 1% per decade. Changes in sea ice alter the extent and distribution of foraging platforms for larger mammals and refuge habitat for smaller species. At the Palmer Peninsula, seasonal sea-ice cover has been shrinking at astonishing rates because of increases in onshore winds driven by hemispheric changes in atmospheric circulation. The duration of sea-ice cover has declined by 85 days since 1978 (Stammerjohn et al. 2008).

Seasonal lake and river ice occur in all temperate regions, with durations of days to months, whereas perennial ice cover is only found at extremely high latitudes and elevations. The date of lake-ice formation and breakup is commonly recorded for commercial purposes related to shipping, trapping, fishing, ice harvesting, and transportation and yields an extensive long-term record (Magnusson et al. 2000). Since 1846, lake-ice duration in the Northern Hemisphere has decreased by 12 days per century, which is equivalent to a warming of 1.2°C per century. A 20-year record of ice thickness in late March on an alpine lake in the Niwot Ridge LTER site shows a consistent thinning of the ice cover at 2.0 cm per year (Caine 2002). Ice cover exhibits strong control over exchanges in gases and material, solar radiation, and heat between aquatic habitats and the atmosphere. The duration of ice exerts a profound influence on the patterns of water circulation and thermal stratification, which are closely linked to the life cycles of aquatic organisms and to the biogeochemical cycling of the ecosystem.

Snow (figure 2d) is the largest component of the cryosphere in areal extent. About 98% of the snow-covered land on Earth is in the Northern Hemisphere, which contains nearly half of the planet’s land surface. In the Southern Hemisphere, over 99% of the snow cover is confined to Antarctica and largely consists of perennial snow. In the Northern Hemisphere, strong negative trends in the extent of snow cover have been observed over recent decades (Dery and Brown 2007). Increased snowfall and snow depth have been reported at the highest-elevation sites of the western United States (Williams et al. 1996); however, most locations in the Mountain West have experienced snowpack declines, and concern has risen about streamflow, water yields, and water supply. In the Pacific Northwest, extensive snow-covered regions are now deemed at risk in terms of their capacity to provide reliable water yields because of atmospheric warming, altitudinal shifts in the distribution of snow and rain, and declining winter snowpacks (Nolin and Daly 2006). Winter snow depths have also been decreasing throughout the northeastern United States. For example, at the Hubbard Brook LTER site in New Hampshire, the maximum snow depth has declined by 25 cm (7 cm water equivalent), and snow cover duration has decreased by 21 days over the past 53 years (Campbell et al. 2010), which has led to major changes in terrestrial and aquatic ecosystems.

One simple metric in the attempt to capture potential ecosystem vulnerability to changes in the cryosphere across ecosystems is the duration of frost and freezing temperatures (table 2, figure 3). Frost days are those with long-term mean daily minimum temperatures below 0°C; freeze days are those with long-term mean daily maximum temperatures below 0°C. Vulnerability can be thought of as susceptible to increased or decreased frost or freezing periods. For example, ecosystems that do not experience frost, such as those in the tropics, are highly vulnerable to cold temperatures. Significant ecosystem changes could be expected if the climate were to cool, making frost commonplace. Alternatively, ecosystems accustomed to long frozen periods, such as polar and high alpine ecosystems, are highly vulnerable to warm temperatures. Those ecosystems exposed to moderate periods of frost or freezing would be expected to be less vulnerable to changes in temperature. We focus on the warming climate, and as such, the tropical ecosystems will not be directly exposed to cryospheric losses, whereas polar and high alpine ecosystems may be the most vulnerable to such change. In table 2 and figure 3, we can see the vulnerability of the major ecosystem research sites under study by US scientists.

**Ecosystem responses to the loss of snow and ice**

The various components of the cryosphere provide physical habitat for diverse organisms. Iconic examples include polar bears and penguins in sea ice and pikas in rock glaciers (rock debris with ice filling the void spaces between the rocks; the mass flows downhill), but many other species ranging in size from microbes to whales inhabit permafrost, glaciers, sea-ice, and snow-covered landscapes. As these habitats shrink and disappear, resident species are forced to migrate, often tracking the distribution of receding frozen habitats across the landscape. Since different organisms respond and move at different rates (e.g., trees versus penguins), cryosphere recession can have many consequences: the fragmentation of animal and plant communities and the development of new assemblages, disruption of seasonally synchronized phenological connections among species, and losses in biodiversity and the associated changes in ecosystem function (Parmesan 2006). Although these processes are occurring at unprecedented rates in response to rapid climate warming, it has required decades of coordinated observations to document significant change and to uncover the mechanisms linking climate forcing to ecosystem responses.

Prolonged, systematic studies of this type are a key contribution of LTER. The LTER Network of sites facilitates long-term observations, experiments, and comparative studies that enable us to identify common processes and mechanisms across diverse ecosystems. The highly interdisciplinary nature of LTER helps to quickly reveal interpretations of
causes and consequences and needed adjustments of monitoring approaches to catch signals of previously unmonitored or unanticipated system behaviors. Here, we present some notable examples of ecological and biogeochemical changes in response to cryosphere loss.

**Changes in populations and trophodynamic implications.** Decadal-scale declines or distributional shifts in snow- and ice-dependent species are now extensive and well documented (Chapin et al. 2005). When ice-dependent species suffer habitat loss, the changes in frozen habitats (glaciers, sea ice, snowpacks, and permafrost) impose both bottom-up and top-down forcings on terrestrial and aquatic ecosystems. Ice loss affects ecosystems directly through the loss of physical habitat and through alterations in thermal conditions and indirectly by altering light and nutrient supply to primary producers. Both Arctic and Antarctic sea ice harbor a resident microbial community of diatoms, other phytoplankton, bacteria, and protozoan grazers that contributes to the total primary production of polar seas. Like sea ice, ice and rock glaciers are habitats for specially adapted species that may disappear as glaciers retreat and their cold, glacier-fed streams disappear. The American pika (*Ochotona princeps*)—although it is not as well known or charismatic as penguins or polar bears—is attaining new status as a poster child for glacier loss and climate change. Pikas do not hibernate and use subsurface microclimates in rocky debris to persist where surface conditions would preclude their survival. Despite this adaptation, some local pika extinctions in the Northwest have been linked to cold exposure caused by a loss of insulating snow cover (Ray et al. 2012). Permafrost thaw also results in habitat disappearance for its resident species. Because permafrost occurs in so many different habitats in different stages of development, its loss may trigger primary or secondary successions.

Widespread past and projected future reductions in snow-cover extent, duration, depth, and water equivalent can also have extensive ecological repercussions. Many plant and animal species are adapted to snow-cover conditions and will perish if they are unable to migrate or tolerate less snow cover. Even so, not all animals that live in cold environments respond negatively to reductions in snow cover. For example, ungulates such as white-tailed deer, mule deer, elk, and caribou expend less energy and are less susceptible to predation when snowpacks are shallower. Some of the species most susceptible to snow-cover loss

### Table 2. Cryosphere processes at US Long Term Ecological Research (LTER) Network sites and related LTER sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Abbreviation</th>
<th>Record</th>
<th>Continental glacier</th>
<th>Alpine glacier</th>
<th>Sea ice</th>
<th>Lake ice</th>
<th>Continuous permafrost</th>
<th>Discontinuous permafrost</th>
<th>Seasonal snow</th>
<th>Transient snow</th>
</tr>
</thead>
<tbody>
<tr>
<td>McMurdo</td>
<td>MCM</td>
<td>1988–2009</td>
<td>X</td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arctic Tundra</td>
<td>ARC</td>
<td>1988–2008</td>
<td></td>
<td></td>
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<tr>
<td>Niwot Ridge</td>
<td>NWT</td>
<td>1952–2006</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Bonanza Creek</td>
<td>BNZ</td>
<td>1988–2009</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Palmer</td>
<td>PAL</td>
<td>1989–2010</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Loch Vale</td>
<td>LWL</td>
<td>1993–2008</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
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<tr>
<td>Marcell</td>
<td>MAR</td>
<td>1961–2010</td>
<td></td>
<td></td>
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<tr>
<td>North Temperate Lakes</td>
<td>NTL</td>
<td>1978–2010</td>
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<tr>
<td>Hubbard Brook</td>
<td>HBR</td>
<td>1964–2007</td>
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<tr>
<td>Harvard Forest</td>
<td>HFR</td>
<td>1964–2002</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kellogg</td>
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*Note: The superscript number next to the abbreviation refers to the sponsoring agency for that site: 1, US LTER Network site; 2, US Geological Survey Water, Energy, and Biochemical Budgets site; 3, US Department of Agriculture Experimental Forest and Range site; 4, National Wildlife Refuge; 5, State Experimental Forest. Record refers to the length of the air-temperature record used to estimate frost and freezing duration at each location.*
Changes in habitat and productivity regimes can ripple up the trophic ladder, as is demonstrated extensively in marine food webs. Changing snow and ice conditions alter habitat suitability for many bird species (e.g., petrels, Adelie penguins [*Pygoscelis adeliae]*) and limit the physical space available for habitation (Micol and Jouventin 2001, Weimerskirch et al. 2003). The huge populations of krill in Antarctic marginal sea-ice zones serve in turn as a major food resource for a suite of large predators, including seabirds, seals, and whales. Sea-ice microbial communities serve as a principal food source for juvenile krill, which also hide from predators in under-ice cryptic spaces. Therefore, the regional decline in the duration and extent of sea-ice cover in the Bellingshausen and Amundsen Seas has resulted in declining abundance and ranges of Antarctic krill (*Euphausia superba*), possibly the most numerous metazoan species on Earth. Atkinson and colleagues (2004) documented large-scale, order-of-magnitude declines in krill populations over 50 years in the South Atlantic sector of the Antarctic seas. Meanwhile, the number of salps—pelagic, gelatinous, ice-avoiding tunicates with few predators—has increased; they have, in effect, replaced krill as an intermediate species in Antarctic marine food chains. One of the best-studied examples of the response of predator populations to sea-ice loss is the Adelie penguin, a true Antarctic penguin with strong fidelity to sea ice as a platform for foraging activity (Ducklow et al. 2007). Since 1975, Adelie penguins nesting near Palmer Station have declined by about 80% in response to a host of environmental changes, including habitat loss and altered food availability (figure 4). Fraser and Hofmann (2003) demonstrated that penguin chicks weighing less than 300 grams at fledging had a reduced probability of surviving past the first year. They suggested that changes in the sea-ice season shifted the period of maximum krill stocks away from the penguins’ peak foraging season. Over the same period, two subpolar species—chinstrip (*Pygoscelis antarcticus*) and gentoo penguins (*Pygoscelis papua*)—have successfully immigrated to the region and now constitute half of the total penguin population in the region. The mechanisms behind these shifts and their long-term outcome are unclear (Trivelpiece et al. 2011). The recent loss of sea ice could boost primary productivity in the Arctic Ocean by a factor of two or three. In the northern Bering Sea, primary-productivity changes caused by warming

**Figure 3. Duration of frost and freezing periods at LTER and related long-term research sites, from climate records.** See table 2 for the site abbreviations. Frost days are those with long-term mean daily minimum temperatures below 0 degrees Celsius (°C); freeze days are those with long-term mean daily maximum temperatures below 0°C.

are those that overwinter below ground, since snow insulates the subsurface and moderates its temperature. The shortgrass steppe in the western United States receives little snowfall and therefore presents an endpoint in the spectrum of snow cover. At this semiarid, high-elevation site, snowfall from November to late February has little effect on ecological processes; however, large snowfalls in March and April (after the ground has thawed) strongly influence the subsequent productivity by controlling the availability of water and nutrients (Cayan et al. 2001). Some plants are photosynthetically active in shallow spring snowpacks, giving them a competitive advantage in regions with short growing seasons (Starr and Oberbauer 2003). As the climate warms, the disappearance of snow cover and the increased length of the growing season may benefit some plants, provided that other requirements for growth are not limiting. Many plants in alpine and tundra regions are reliant on snow for water and nutrients and therefore are found in the greatest abundance where the range of snow depths is optimal (Walker et al. 1993). Although the snow-free period will lengthen in a warmer climate, the lack of snow cover during colder months will increase soil temperature variation, making roots susceptible to winter injury. Soil freezing can directly and adversely affect roots by causing cellular damage and can also sever fine roots through frost heaving. Reduced nutrient uptake as a result of root injury has been shown to lower nutrient retention and to increase hydrologic fluxes from soils during the growing season (Fitzhugh et al. 2001).
and sea-ice loss have resulted in a dramatic reorganization of the ecosystem (Grebmeier et al. 2006). This shallow marine ecosystem was formerly characterized by high primary productivity and efficient export to the bottom, which supports a high stock of benthic prey for diving ducks and walruses. With the loss of sea ice and the warming of the water column, the export of surface productivity into the benthos has declined, which has caused a switch from a system with top predators sustained by benthic prey to one dominated by pelagic fish.

**Changes in biogeochemical cycles.** Changes in the extent, seasonality, and duration of cryosphere components affect the cycling of nutrients in land and ocean ecosystems. Glacier retreat and rock glacier shrinkage expose new landscapes that are typically carbon poor yet nutrient rich because of rock weathering. Microbial life—particularly nitrogen fixers—occupy these new landscapes (Nemergut et al. 2007), which increases the nitrate levels of streams and lakes down valley. These conditions are transient and slowly change as higher plants occupy the landscape over time scale of decades to centuries. High alpine waters are typically oligotrophic and are therefore susceptible to ecological changes that result from increases in nitrogen export from the land (Baron et al. 2009). Williams and colleagues (2007) characterized the nutrient content in the outflow of the Green Lake 5 rock glacier, located in the Green Lakes Valley of the Colorado Front Range. The nitrate concentrations from the rock glacier are among the highest reported for high-elevation surface waters. These extreme nitrate concentrations appear to be characteristic of rock glacier outflows in the Rocky Mountains (Williams et al. 2007). Fluorescence index values and dissolved organic matter (DOM) measurements are consistent with a switch from terrestrial DOM in the summer to an increasingly aquatic-like microbial source during the autumn months. Glacier melting has also been implicated in the regulation of phytoplankton species composition in Antarctic coastal regions where diatoms—the preferred food for Antarctic krill (see above)—are being replaced by less-palatable cryptophytes. Glacial inputs change light availability by stabilizing the surface-water column and possibly stimulate growth selectively by adding limiting micronutrients (Dierssen et al. 2002). Melting glaciers and sea ice also transfer airborne pollutants stored in the snow and ice to the marine environment.

Perhaps the most important result from the reduction in duration of lake ice in a warming climate is less-frequent oxygen-depletion events and the associated adverse biological consequences (Prowse et al. 2006). For river ice, large fluxes of allochthonous detrital material and nutrients are flushed into the river water column because of channel scour during ice breakup and flooding. Geomorphically, at the Pine Island LTER site in coastal Massachusetts, the formation and transport of river ice are important factors in determining salt marsh platform elevation and have implications for responses to rising sea level. The delivery of sediment to the marsh through ice rafting (Wood et al. 1989), the compression of the marsh surface as a function of ice thickness, and the scour of vegetation are winter processes that will change as less river ice forms and its transport into fringing salt marshes declines in the coming decades.

In cold regions, nutrient cycling is closely coupled with snowpack dynamics, with much of the annual export of stream nutrients occurring in winter, when biological uptake is low. Changes in the snowpack alter hydrology, which affects the amount, timing, and magnitude of spring snowmelt. The resulting changes in streamflow not only affect nutrient transport but, when they are combined with changes in temperature, also affect aquatic habitats, causing potential shifts in species assemblages. Nutrients accumulate in the snowpack over winter and are released in an ionic pulse during the first portion of snowmelt (Johannessen and Henriksen 1978). Although snowmelt can be an important source of nutrients and water early in the growing season, it can also cause episodic acidification in areas with high atmospheric deposition and poorly buffered soils (e.g., Schaefer et al. 1990). The soils beneath the snowpack are also an important source of nutrients during winter and early spring. The snowpack regulates soil temperatures, keeping them warm enough for many biologically mediated reactions. Snow fence experiments, which enhance winter snow accumulation, have shown that higher rates of soil microbial respiration and nitrogen mineralization occur under deeper snowpacks in subalpine forest and Arctic tundra environments because of warmer soil temperatures that result from the thermally insulating effects of the snow (Schimel et al. 2004). In contrast, in boreal spruce and temperate hardwood forests, thin winter snowpacks increase the frequency and depth of soil freezing, which results in elevated summer nitrogen emissions that are probably a result of reduced nitrate uptake by damaged roots and by root decomposition (Fitzhugh et al. 2001, Maljanen et al. 2010). Fluxes of carbon dioxide ($CO_2$) mirror those of nitrogen, and the timing and magnitude of the nitrogen and $CO_2$ fluxes in all cases

Figure 4. Populations of ice-dependent (Adelie) and ice-tolerant (chinstrap and gentoo) penguins near Palmer Station, Antarctica, measured between 1976 and 2009. Source: Adapted from Ducklow and colleagues (2007).
depends on plant species. Elevated nitrogen mineralization contributes significantly to fluxes of greenhouse gases and to the cycling of nitrogen and carbon. In the mixed-grass prairie of North America, greater snowpack increased soil moisture by midsummer, which resulted in increased soil respiration (Chimner and Welker 2005) and increased plant invasions (Blumthel et al. 2008).

But most of the attention to the biogeochemical consequences of cryosphere loss has been focused on the potential for changes in carbon storage and release. Arctic permafrost contains twice the CO₂ found in the atmosphere, which dramatically demonstrates the potential for altering the climate as further warming occurs. Site-specific information can provide some indication as to the future release rate of carbon from thawing permafrost. A recent group of studies was focused on an upland thermokarst site near Denali National Park in Alaska, where changes in plant and soil processes were studied as a function of time since the thermokarst disturbance was initiated. The studies showed that increased permafrost thaw and ground-surface subsidence increased net and gross primary productivity as plant growth was stimulated by a thaw (Vogel et al. 2010). Plant species composition changed along with changes in plant growth rates as graminoid-dominated moist acidic tundra shifted to shrub-dominated tundra with increased rates of thawing. The increased carbon uptake by plants initially offset the greater ecosystem respiration, such that this thermokarst was a net sink of carbon 15 years after the initiation of the thaw, even though decomposition of older carbon deep in the soil was already occurring (Schuur et al. 2009). Over more decades of thaw, plant growth rates remained high, but increased old soil carbon losses eventually offset the greater carbon uptake, and this thermokarst become a net source of carbon to the atmosphere.

In a contrasting study of lowland thermokarst in three Canadian peatlands, the carbon accumulation in surface soil organic matter was higher in unfrozen bogs and in areas where permafrost had degraded than in areas where permafrost was intact (Turetsky et al. 2007). This growth in surface soil carbon accumulation was consistent with the Alaskan upland study, but the equivalent net ecosystem carbon exchange measurements were not available to determine whether the thawed permafrost peat ecosystems were overall net sources or sinks of carbon. Permafrost thaw in this lowland system promoted the release of methane (CH₄) because waterlogged conditions predominated in Sphagnum moss lawns that replaced the feather moss (Hylocomium splendens) and black spruce (Picea mariana) forest in locations where permafrost degraded. This CH₄ release was hypothesized to potentially offset the observed surface soil carbon accumulation for at least for 70 years, until plant and ecosystem succession in the moss lawn created conditions more like those in the unfrozen bogs, which stored surface soil carbon but released only small amounts of CH₄. The release of CH₄ is a common pathway of carbon loss in lowland thermokarst, where drainage is restricted (Myers-Smith et al. 2007), and CH₄ has 25 times greater heat-trapping capacity than CO₂ on a century timescale. However, decreased total carbon emissions in anaerobic systems can partially offset the increased radiative forcing of CH₄ release, which possibly makes the net radiative forcing of increased carbon losses in lowland and upland thermokarst more similar than what the difference in heat-trapping capacity between CO₂ and CH₄ would initially suggest.

The oceanic sink for anthropogenic CO₂ is large and lessens the potential greenhouse effect by limiting CO₂ accumulation in the atmosphere. The current (2009) net annual carbon uptake by the ocean is 2.3 ± 0.4 petagrams (Pg) of carbon per year, compared to 2.4 Pg of carbon per year for land, but the land uptake is partially offset by the 1.1 ± 0.7 Pg of carbon per year in releases caused by deforestation (Le Quéré et al. 2009). As the ocean warms and its inventory of CO₂ increases, the oceanic sink is expected to weaken. Oceanic CO₂ uptake is governed by gas exchange across the air–sea interface, so the regional allocation of CO₂ uptake is primarily a function of the area of sea surface involved. This fraction has been predicted to increase as ice melts and productivity increases, which will expose new ocean areas to solar irradiance (Peck et al. 2010). The Arctic Ocean constitutes just 3% of the total ocean area and is mostly covered by sea ice, which blocks gas exchange, but it accounts for 5%–14% of the total ocean CO₂ uptake. New observations suggest, however, that the recent dramatic loss of sea ice has been accompanied by decreased rather than increased CO₂ uptake (Cai et al. 2010), which is counter to current understanding and predictions. The rapid, diverse, and complex changes wrought by cryosphere loss constitute a major scientific challenge that demands new large-scale observing systems on land and in the ocean to provide new observational infrastructure as a resource for coordinated experimental studies performed by the LTER Network and other scientists.

**Effects on humans from the loss of snow and ice**

Cryosphere loss will result in far-reaching social, economic, and geopolitical impacts, but a detailed treatment is beyond the scope of this synthesis. Most attention has been devoted to the impacts associated with a loss of snow cover, glacier melting, and sea-level rise, which are treated elsewhere (Kundzewicz et al. 2007). Thawing permafrost will also have important social consequences, because it can destabilize engineered structures and can cause destructive slides, flows, and slumps. Changes in snow cover can have important consequences for humans and may affect many diverse activities, including agriculture, recreation, tourism, engineering, commerce, and energy production. For example, the New Hampshire ski industry has abandoned low-elevation ski areas in the southern part of the state since the 1970s, in part because of climate warming, in favor of ski areas at higher elevations in the north (Hamilton et al. 2003). Skiing contributes about $1 billion annually to the economy of Utah, but recent climate change
evaluations of the ski industry there suggest that it is at risk in the next several decades (Lazar and Williams 2008). A similar impact is anticipated for the Pacific Northwest. The most important effect is the influence on streamflow. In many semiarid regions of the world, such as the southwestern United States, snowmelt from mountain snowpacks is the dominant source of water for human consumption and irrigation. Therefore, changes in the amount and timing of snowmelt in mountainous areas could affect stream ecosystem services, such as drinking-water supply, wastewater assimilation, and hydropower. Lesser amounts of snow could also have an impact on agriculture and the ability to produce food, both through an increased occurrence of drought and through an inadequate supply of water for irrigation. Some evidence suggests that changes in snowmelt may also increase the risk of forest fires. In the western United States, earlier snowmelt dates correspond to increased wildfire frequency, because soils and vegetation are becoming drier and the period of potential ignition is lengthening (Westerling et al. 2006). Estimates of sea-level rise to 2100 have been continually revised upward since the 2007 report of the Intergovernmental Panel on Climate Change (Solomon et al. 2007) as new data and modeling have been developed. At the time of this writing, the rise in sea level by the end of the century is projected to be about 1 m (Pfeffer et al. 2008). The economic cost of a 1-m rise in sea level is estimated to exceed $1 trillion (Anthoff et al. 2010), with enormous social and political dislocations as residents of low-lying regions are forced to move to higher ground.

The Arctic has emerged as a key laboratory for the study of climate change impacts on human communities, partly because it is host to the world’s largest indigenous population that maintains a subsistence lifestyle (Kofinas et al. 2010) and partly because of the rapidly manifesting impacts on infrastructure, transportation, and international relations. The complex interplay among climate, biogeochemical, ecological, and sociopolitical factors responding to cryosphere loss in the Arctic and around the world demands new levels of interdisciplinary collaboration and new models for scientific study (Driscoll et al. 2012 [in this issue]). A system-level understanding of the global cryosphere is fundamental to predicting the future course of the Earth’s socioecological system and to laying out a course for human social, political, and economic adaptation to climate change.

As was demonstrated in this article and others in this issue, socioecological ecosystem science as pioneered by the US LTER Network is a key component of our current and future understanding of cryospheric change.

Conclusions
Earth is distinguished in the solar system by the coexistence of water in its three phases: solid (frozen), liquid (melted), and gas (evaporated). The solid phase—the global cryosphere in all its components: glaciers; snow; permafrost; sea, lake, and river ice—is arguably the most rapidly changing element of the Earth system. Cryosphere loss can be viewed as a planetary-scale redistribution of solid water into its liquid and gas phases. This large-scale reorganization will trigger changes in the balance of positive and negative feedbacks in the climate system (e.g., changes in planetary albedo), with far-reaching consequences for ecosystems and society, including changes in sea level, precipitation, and water availability. The current geophysical rates of cryosphere loss are now well documented but our lack in understanding of the relevant mechanisms limits our ability to predict the future course of change, with potentially grave consequences for society. In particular, we lack long-term observations and system-level experiments in which the linkages between changes in physical habitat and climate on one hand and ecosystem structure and biogeochemical functions on the other are addressed. LTER Network sites have pioneered coordinated observations and experimental manipulations of ecosystems and elemental cycles (Knapp et al. 2012 [in this issue]). An expansion of our fundamental knowledge of the phenologies and processes governing ecosystem responses to climate change is a necessary first step in creating future scenarios of change and human responses to it (Thompson et al. 2012 [in this issue]). This new understanding will continue to come from LTER sites situated in all the major cryosphere systems (table 1).

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