

Long Term Ecological Research Network Decadal Review Self Study



prepared by:

The 2019 Decadal Self Study Committee

Peter Groffman, Chair

Baltimore Ecosystem Study LTER and Hubbard Brook LTER, City University of New York and Cary
Institute of Ecosystem Studies

Deron Burkepile

Moorea Coral Reef LTER, University of California-Santa Barbara

Frank Davis

LTER Network Office, University of California, Santa Barbara

Martha Downs

LTER Network Office, University of California, Santa Barbara

David Foster

Harvard Forest LTER, Harvard University

Michael Gooseff

McMurdo Dry Valleys LTER, University of Colorado, Boulder

Corinna Gries

Environmental Data Initiative, North Temperate Lakes LTER, University of Wisconsin

Sarah Hobbie

Cedar Creek LTER, University of Minnesota

Jennifer Lau

Kellogg Biological Station LTER, University of Indiana

James McClelland

Beaufort Lagoon Ecosystems LTER, University of Texas

To the Review Committee:

We are delighted to present materials for your consideration during the fourth decadal review of the U.S. National Science Foundation (NSF) Long Term Ecological Research (LTER) program. To aid in your assessment of the program's recent progress, we have assembled information on the Network's activities over the past 10 years, including:

- An executive summary
- A general introduction to the LTER Network
- A letter responding to the 30-year review recommendations and NSF's related guidance
- A series of eight thematic narratives illustrating how LTER funding has facilitated unique and important scientific findings and societal impacts, focusing on:
 - Nutrient supply effects on ecosystems
 - Consumer controls on communities and ecosystems
 - The role of historical legacies in today's ecosystems
 - Biodiversity-ecosystem functioning relationships
 - Physical, chemical and biological connectivity
 - Coupled social-ecological science
 - Resistance, resilience, and state change
 - Evolution in long term ecological experiments
- Two summaries describing the recent work of the Information Management and Education committees
- 28 short summaries from each site, highlighting the nature and extent of the research in the LTER Network

We hope that these materials reflect our appreciation of the opportunity presented by LTER funding and our pride in the accomplishments of the Network. We recognize the time and effort that goes into reviewing a program as extensive as LTER and look forward to your insights and reflections.

Sincerely,

Peter Groffman,

Hubbard Brook Ecosystem Study LTER, City University of New York and Cary Institute of Ecosystem Studies

On behalf of the Self Study Committee, the LTER Science Council, and the LTER Network

Table of Contents

1	Executive Summary	1
2	Introduction.....	6
3	Response to the 30-year Review.....	14
4	LTERR Science Advances: Selected Themes and Examples	22
5	Nutrient Supply Effects on Ecosystems	23
6	Consumer Controls on Communities and Ecosystems	28
7	The Role of Historical Legacies in Today's Ecosystems.....	32
8	Biodiversity-Ecosystem Functioning Relationships	36
9	Physical, Chemical, and Biological Connectivity.....	41
10	Coupled Social-Ecological Systems	45
11	Resistance, Resilience & State Change	50
12	Evolution in Long Term Ecological Experiments	56
13	Information Management in the U.S. LTER Network.....	61
14	Education and Outreach in the U.S. LTER Network.....	65
15	Site Briefs	67
16	References.....	177

1 Executive Summary

Since its establishment by the National Science Foundation in 1980, the Long Term Ecological Research Network has been a major force in the field of ecology. LTER researchers have addressed fundamental questions about how ecosystems work, established seminal ecosystem experiments; maintained long term observations of ecosystem variables; and significantly advanced ecological theory and predictive models. Long term ecological research is an engine for developing and testing ecological theory¹ (Figure 1.1). The sustained involvement of large teams of active scientists has also delivered substantial and ongoing engagement with resource managers, policymakers, educators, and public audiences – making the LTER a key resource for evidence-based environmental policy and knowledge at all levels.

As the Network approaches its 40th anniversary, this self-assessment reports major achievements for the decade 2009-2018, to inform the work of the decadal review committee. It includes three major components: (1) highlights of the work the Network has done to respond to the 30-year review of the program, (2) a synthesis of eight major scientific themes where long term research is especially valuable and where LTER research has made significant advances, with highlighted examples of achievements, and (3) site briefs summarizing key activities, contributions, and

research products for each of 28 sites that was active during the reporting period.

Our overall assessment is that the LTER Network has continued to play an outsized role in the science of ecology, moving the frontier of ecological theory while discovering and characterizing operative ecosystem processes. LTER research has been extraordinarily productive and contributed not only to ecology but also to climate science, oceanography, hydrology, and complex systems – to address some of the most pressing issues facing society.

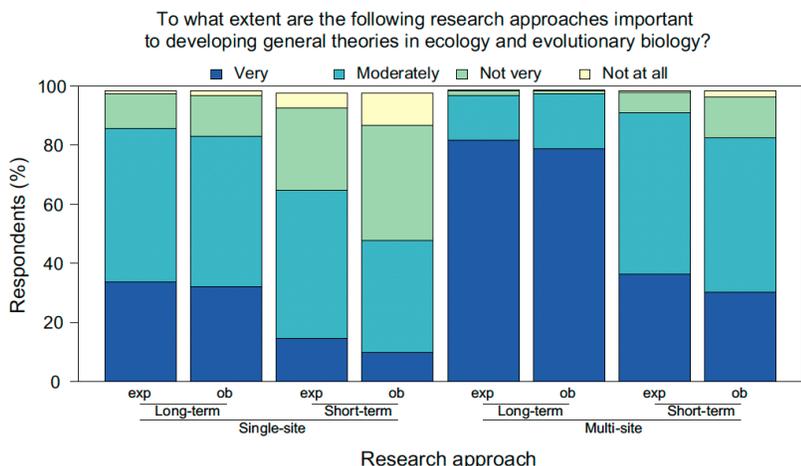


Figure 1.1. An independent survey of 1,179 ecologists and evolutionary biologists working in 31 subfields found that long-term, multi-site, observational (ob) and experimental (ex) research were the most frequently cited research approaches considered “very important” for developing general theories in ecology and evolutionary biology. From Kuebbing et al 2018.

In 2019, the Network includes 28 sites (7 coastal, 6 forest, 5 grassland, 4 marine, 2 freshwater, 2 urban, 1 alpine, and 1 tundra) and a network office (Figure 1.2). At any given time, thousands of personnel – including more than 1000 investigators, 600-800 graduate students, many hundreds of undergraduates, and thousands of K-12 students – are engaged in a host of LTER research, education, and outreach activities. Over the past decade, NSF’s funding for the LTER Program has remained relatively steady at ~\$30 million annually. Program funding has been well-leveraged with

other funds from both NSF and non-NSF sources, including DOE, NASA, USFS, EPA, state agencies, and private foundations such that total funding across sites has averaged more than \$90 million annually.

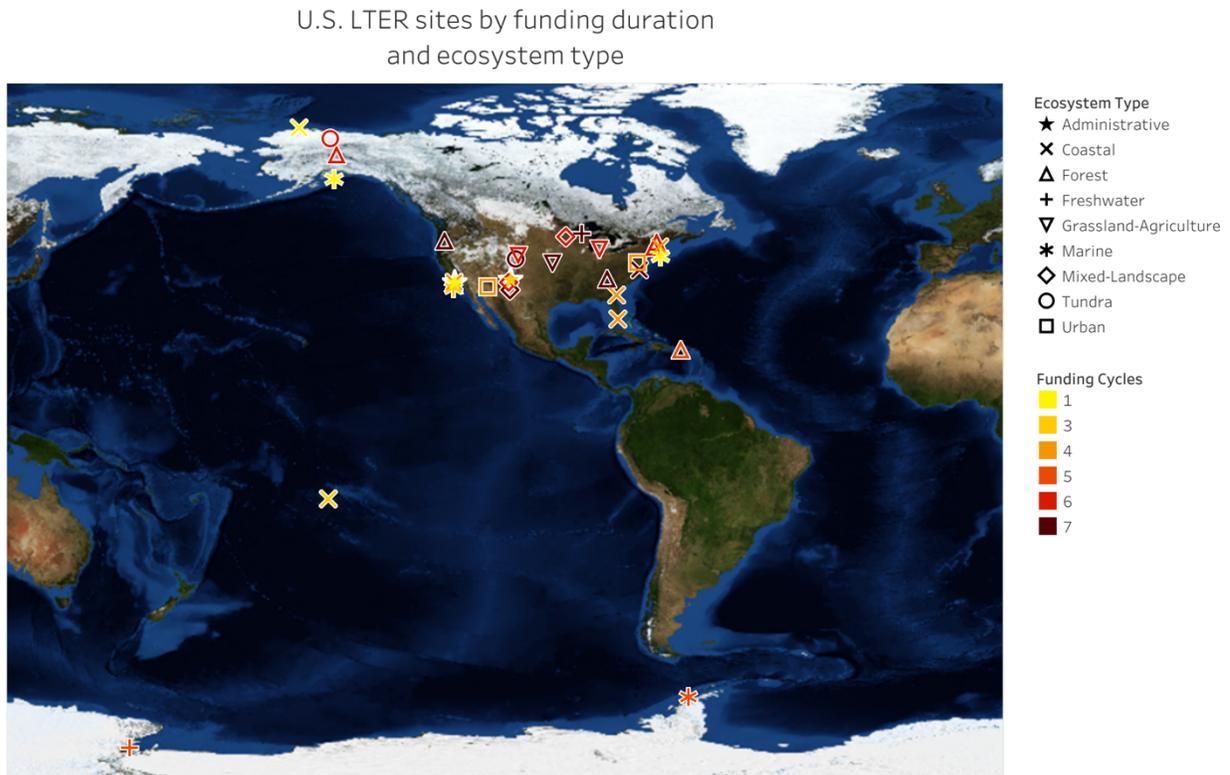


Figure 1-2. Long Term Ecological Research (LTER) sites by ecosystem type and site funding duration, as of September, 2019.

Over the last 10 years, LTER research products included, but were not limited to, 700-800 journal articles and 90-100 graduate theses per year. Rather than attempting to summarize the entire corpus of LTER research over the past decade, we present selected examples of LTER's recent groundbreaking research in eight thematic areas:

1. **Nutrient supply effects on ecosystems.** Nutrients are now mobilized and transported around the globe on a massive scale. Patterns of precipitation are changing dramatically. Long term experiments in many ecosystems are yielding a mechanistic understanding of how ecosystem productivity and stability respond to changing and more variable resources. LTER researchers have shown that short term ecosystem responses to nutrient addition may have little bearing on decadal-scale direction and magnitude of nutrient effects. Moreover, nutrient-induced changes in community composition may persist for many years after the cessation of experimental nutrient additions. These insights have provided important guidance for managing water quality, ecosystem health, and production in aquatic and terrestrial ecosystems.
2. **Consumer controls on communities and ecosystems.** The role of herbivores and predators in controlling community composition, nutrient cycling, and energy and material transfers across landscapes offers some of the greatest surprises in ecology. Effects can be complex, non-linear,

and difficult to assess with short term data. Consumer effects have been examined by LTER scientists in diverse ecosystems ranging from grasslands to boreal forests to estuarine and coastal marine ecosystems. Consumers have been shown to change the course of ecosystem recovery from disturbance, alter plant competitive interactions, affect long term patterns of lake eutrophication, and influence rates of carbon sequestration. This research has significant broader impacts given that consumers are heavily exploited across most ecosystems on Earth.

3. **The role of historical legacies in today's ecosystems.** Lasting effects of historical events – such as past agriculture in currently forested or semi-natural ecosystems, logging, air and water pollution – on today's ecosystems are well documented at many LTER sites. For example, acid rain has abated in New England but research at Hubbard Brook has shown that the effect of soil calcium depletion may last for centuries. Despite improved agricultural source control, legacy phosphorus in sediments of north temperate lakes like Lake Mendota in Wisconsin could continue to impair water quality for decades. Even more recent legacies, such as consecutive years of above- or below-average rainfall or climate-driven changes in fire frequency and severity, can confound interpretation of short term ecological studies. LTER research on legacies has yielded fundamental insights into factors controlling ecosystem resilience, biodiversity dynamics and exotic species invasions while also providing essential context for short term research.
4. **Biodiversity-ecosystem functioning relationships.** It's easy to think that many species may be redundant in their functions. Yet LTER experiments have established myriad affirmative relationships between biodiversity and valuable ecosystem processes including productivity, stability, pest control and carbon sequestration. Some biodiversity effects have taken a decade or longer to manifest; for example, the positive relationship between plant community richness and soil microbial communities and carbon stocks. Cross-site synthesis based on decades of data has revealed the positive influence of biodiversity on temporal stability of ecosystem net primary production. Researchers have also linked not only diversity but community composition and individual species to ecosystem processes at large scales, highlighting the role of “foundation” species such as kelp, eastern hemlock, and eelgrass in creating specific abiotic and biotic ecosystem properties.
5. **Physical, chemical and biological connectivity.** We live in a connected world. African dust fertilizes forest and crop growth in the U.S., Midwest agriculture drives water quality concerns in the Gulf of Mexico and global shipping introduces environmental management challenges everywhere. While the LTER Network is defined by temporal duration, its multidisciplinary teams and geographic extent present an ideal staging for research to understand connections between landscape elements, ecosystem compartments, and continental-scale interactions. Major projects to untangle global linkages, such as the Arctic Great Rivers Observatory, have strong roots in LTER science. Current examples of LTER connectivity research include genetic studies of southern California kelp forests by the Santa Barbara Coastal LTER, revealing that kelp clusters function as a metapopulation where better-connected reefs recover more quickly from local storm-caused kelp eradication than more isolated reefs. Connectivity research is also integral to predicting the effects of sea level rise and hurricane impacts, as shown by studies at the Georgia Coastal Ecosystem LTER, and of climate change impacts at the Arctic and Niwot Ridge LTERs, where significant changes in river chemistry have been linked to thawing permafrost and the mobilization of long-stabilized organic carbon.

6. **Coupled social-ecological systems.** Many LTER researchers and sites have helped to drive and inform a scientific paradigm shift away from treating humans as exogenous drivers of ecosystem change towards considering them as interactive components of ecosystems. For example, the long-running social surveys at urban LTER sites in Phoenix and Baltimore have provided novel information on environmental knowledge, perceptions, values, and behaviors; how these influence ecosystem structure and function; and how changes in ecosystem structure and function may affect physical activity, social cohesion, perception of neighborhood desirability, and willingness to relocate. Understanding feedbacks between environmental change and human behavior is not limited to urban LTER sites; in fact, many sites have engaged in interdisciplinary studies of human-environment interactions ranging from research on decision making by farmer and forest owners to co-production with local stakeholders of regional social-ecological scenarios. This research has offered numerous entry points for LTER science to engage with diverse publics and to inform regional policy and management.
7. **Resilience, resilience and state change.** Ecological tipping points – in which a gradual change culminates in a sudden and stubborn flip, say from coral reef to algae-covered rocks or spruce forest to hardwoods – has been a major theme of ecological research over the past two decades. Long term research has been instrumental in identifying the feedbacks that drive and maintain these disruptive shifts. LTER investigators are also among the first to devise approaches for predicting the onset of a sudden state change. LTER sites have demonstrated the existence of ecosystem hysteresis, in which an ecosystem can exist in alternative stable states depending on disturbance magnitude and initial post-disturbance conditions. A compelling example of such ecosystem hysteresis has been documented at Moorea Coral Reef, where the switch to an algal-dominated state after an extreme event depends in part on the level of fish herbivory, which is largely controlled by human fishing pressure.
8. **Evolution in long term ecological experiments.** LTER's long term, large-scale experiments provide exceptional opportunities to perform controlled evolution experiments in the wild. Such research is of both fundamental and management interest as we seek to understand how species can or will adapt to rapid climate change. Directional selection has been observed in black grama grass under extreme drought at the Sevilleta LTER and potentially by corals recovering from extreme disturbances at Moorea Coral Reef. At Kellogg Biological Station, genetic studies have been used to test predictions of co-evolved mutualism between nitrogen-fixing rhizobia and plant hosts under experimental nitrogen additions. Selective adaptation to atmospheric CO₂ enrichment has been linked to community-level biodiversity at Cedar Creek. Rapid evolution among fungal decomposers under nitrogen addition has been documented at Harvard Forest. Leveraging LTER experiments to study evolution is one of the most exciting new directions for the Network.

The reach and impact of LTER science is being extended through the community's leadership in making data publicly available and using those data in synthesis. During the last ten years, LTER information managers conceived and implemented a comprehensive network-wide data repository providing consistent access to all LTER data and high-quality scientific metadata. The Environmental Data Initiative repository is now fully operational and available to the broader environmental science community. The repository provides access to more than 7,000 unique and original data packages contributed by LTER, including publication-related data and irreplaceable core datasets without which many current synthesis efforts would be impossible. LTER subscribes to the "FAIR" data

principles (findable, accessible, interoperable, and reusable), with machine-readable and -actionable data and metadata, industry standards for data access, a controlled vocabulary, and automated quality checking of metadata. Since 2013, LTER datasets have received digital object identifiers (DOIs) allowing formal citation and – ultimately – usage tracking.

The return on NSF’s investment in long term research through the LTER program has been enormous – not only in terms of scientific discovery, but also in terms of attracting young people to STEM and to research, formal and informal education, the creation and use of shared ecological knowledge with conservation and natural resource managers, and numerous other societal impacts of LTER research. Core LTER grants provide direct stipend support for a few graduate students and undergraduates at each site, but the number of students who benefit from LTER activities is far greater, whether they use LTER data to establish a reference standard, base a thesis chapter on synthesis of data collected from large-scale experiments started before they were born, or participate in education and management partnerships that are nurtured by LTER personnel.

Education programs at LTER sites are highly entrepreneurial, leveraging NSF support to craft effective regional partnerships with public schools, museums, outdoor organizations, and environmental educators. Working through organizational and personal collaborations, they establish programs that support STEM experiences for young people, data literacy programs, teacher resources and research experiences, and art-science collaborations at many sites. Citizen science and K-12 projects are effectively engaging underrepresented communities unique to each site, including native Alaskan hunters and fishers at Bonanza Creek, public school teachers in Baltimore, and more than 15,000 largely Hispanic students at the Asombro Institute for Science Education, which partners with the Jornada LTER. At the network level, education and outreach efforts are focused on themes of data literacy; REU/RET recruitment, inclusive mentoring, and support; and engagement with landowners, environmental planners, and resource management professionals.

Entering the fifth decade of the LTER program, the Network is poised for even greater impact and influence. The recent increase in the number of coastal and ocean sites has broadened the representation of ecosystems in the LTER Network. New methods, such as genomics, high-frequency sensors, autonomous observing systems, animal tracking technology, and new modes of remote sensing, are allowing researchers to collect data at a pace and from locations and scales that previously were impractical or even impossible. Investments in environmental data science and cyberinfrastructure enable broader collaborations and synthesis. Complementary networks, such as NEON, CZO, GLEON, and ILTER, create new opportunities to test at continental and global scales the principles that emerge from LTER inquiry. The LTER platform continues to serve as a magnet for graduate students, postdocs, and early career faculty with ambitious research agendas.

Advances in LTER research over the past 10 years have improved our ability to make and test specific predictions about ecosystems and to work with managers to apply that knowledge for the benefit of humans and ecosystems. As our nation and our world face unprecedented changes, sustaining ecosystem function and services will depend upon a clear understanding of the mechanisms that underlie ecosystem change, resilience, and recovery. The LTER Network – bursting with robust long term studies specifically designed to reveal the ecological mechanisms connecting drivers with outcomes – is uniquely able to advance that understanding.

2 Introduction

In the late 1970's, when the National Science Foundation (NSF) first considered funding long term sites for ecological research, the standard mechanism for funding ecological studies was a three-year grant, barely enough to capture an average value for ecosystem processes. Today, the prescience of the decision to fund studies that allow us to track and understand ecosystem variability, dynamics and responses to environmental change and disturbance processes is abundantly clear. Long term, place-based, question-driven research has proven to be a rich source of new ecological theory, an effective approach for improving ecosystem management, and a resource for training a new generation of integrative environmental researchers.

NSF launched the Long Term Ecological Research (LTER) program in 1980 by funding 6 sites with 5-year continuing grants. Groups of researchers were to receive predictable funding to “focus on a series of core research topics, coordinate their studies across sites, utilize documented and comparable methods, and be committed to the continuation of the work for the required time”². The LTER program benefited from past experiences in establishing platforms for long term ecological research, notably the International Biosphere Program (1968 - 1974) and studies established by visionary ecologists and managers, such as those at Hubbard Brook, Coweeta, and North Temperate Lakes. Five core research areas (primary production, populations, organic matter dynamics, inorganic nutrient cycling, disturbance) facilitated – and continue to facilitate - comparison among and across sites in the Network. A new book in the LTER publication series, expected in 2020, describes the emergence of these ideas and programs in detail.

The program expanded quickly, adding grassland, forest, Arctic, and Antarctic sites in rapid succession over the next 20 years (Figure 2.1) as well as terminating a few sites. At the first site renewals, NSF standardized funding and review cycles so that sites were critically reviewed at 3-year intervals and faced performance-based renewal on a 6-year cycle. Gradually, expectations were clarified and, starting in 1988, a Network Office began facilitating collaboration and synthesis among the sites. From 1998-2005, with the growing recognition of the great value of long-term research to science and society, NSF expanded the program's breadth and potential for comparative and synthetic studies by adding two urban and five coastal and ocean sites. The most recent decade has seen additional turnover with three marine sites added and three terrestrial sites terminated.

2.1 Character of the Research

LTER research is anchored in exemplary place-based science, with projects evaluated based on individual site-based proposals and accomplishments. Thus, each research team chooses questions, measurements, experiments, and models that are tailored to investigating multi-decadal ecological processes in specific ecosystems and landscapes. At the same time, several mechanisms enable LTER researchers and the scientific community to synthesize across sites and systems, across the larger network, and beyond. Site PIs meet annually at Science Council meetings that rotate among site locations, eliciting new questions and unexpected connections. Triennial “All Scientists’ Meetings” bring hundreds of researchers, including many students and early-career scientists, from inside and outside the LTER Network together to forge a culture of long term research, share ideas, foster cross-site collaboration, and mentor an interdisciplinary generation of long term scientists. The

Network Office administers funding for cross-site synthesis research that is often conceived at these two types of meetings.

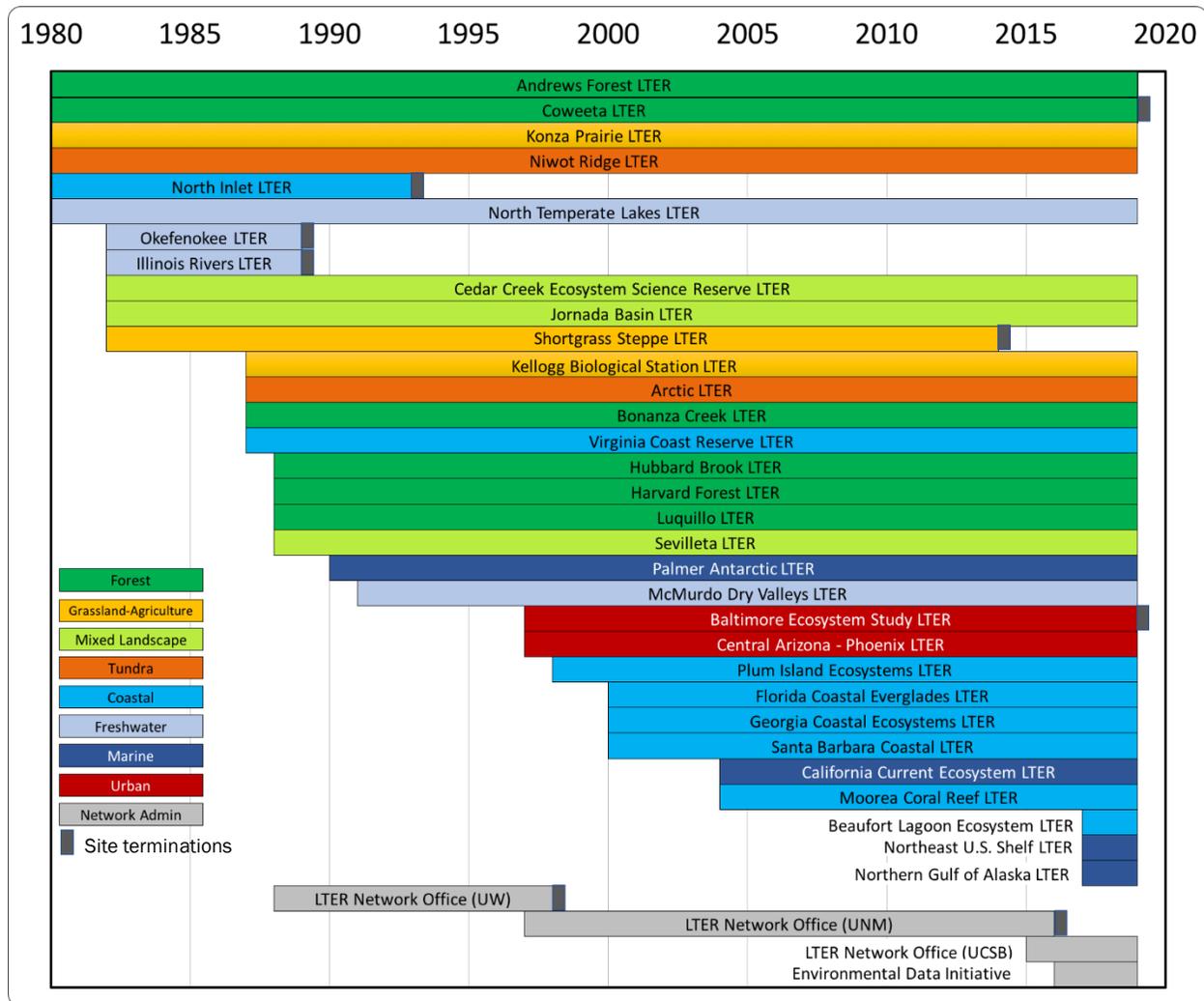


Figure 2-1. Growth and change of the LTER Network, 1980-2020.

From the beginning, LTER sites were seen as platforms that could stimulate and host a wide variety of other studies that might, or might not, require long term funding. Many other research programs – funded by NSF, DOE, NASA, USDA and other agencies and entities – have capitalized on the deep knowledge of LTER researchers, the trove of LTER data, and the research platform provided by long term LTER measurements and experiments to learn more and do more than they otherwise could (Figure 2.2). At the same time, LTER funding directly supports only a fraction of the research that each site team undertakes. This web of interdependence is challenging to unravel fully, but Figure 2.2 provides a sense of the myriad sources of support for science that is LTER-related (that is, that depends on the personnel, data, experiments, or field support of LTER sites). In sum, only 34% of all LTER-related research is funded directly by the NSF LTER program; the NSF LTER budget investment is matched at least 3-fold, largely because of the resources and opportunities that LTER sites provide to science and education.

Sources of funding to LTER sites
2008-2018 | Total=\$912 M

Type
■ NSF
■ other federal
■ non federal

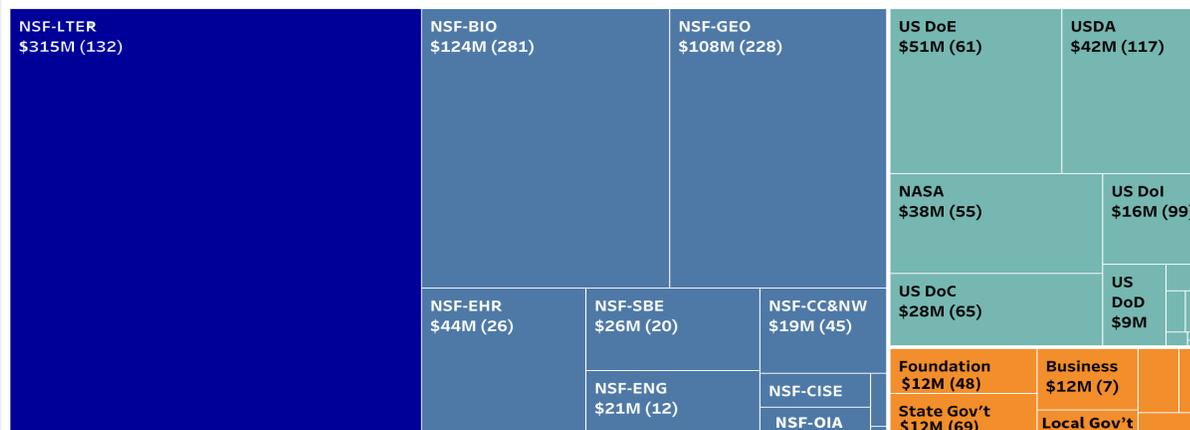


Figure 2-2. Sources of funding to the LTER program 2008-2018. Blue blocks: NSF funding sources (bright blue: LTER program); Teal blocks: Other federal funding sources; orange blocks: non-federal funding sources. Institutional support to LTER programs could not be adequately estimated and is not included here.

2.2 An Ambitious Agenda

Foundational ecological concepts, such as resilience, resource limitation, legacies of disturbance, and diversity-stability relationships were major targets of investigation for the first sites. LTER researchers quickly established ambitious experiments – including whole-ecosystem nutrient additions and physical disturbances, alternate management regimes, and grazer exclusions – to test the strength and generality of hypothesized relationships.

At the same time, sites set up rigorous measurement protocols that allow for the detection and quantification of short and long term changes in populations, community structure, and nutrient and carbon budgets, whether driven by natural variation or anthropogenic change. With measurement systems in place and conceptual models serving as null hypotheses, LTERs are uniquely well-positioned to observe changes in ecosystem processes driven by extreme events and to identify lagging responses to disturbance. With multidisciplinary teams of researchers focusing on diverse landscapes, connectivity quickly became a recurrent theme, whether mediated by movement of water, gas exchange, human commerce, microbial communities, or animals.

Human influence on ecological functioning has been an important aspect of LTER research from the start. However, social-ecological research, which investigates the full range of bidirectional influences between complex social and ecological systems, only became a major emphasis after the 1997 funding of the Baltimore and Phoenix urban LTER sites, which coincided with a major global expansion of urban ecology and sustainability science and prompted the addition of land use/land cover change and human-environment interactions as LTER core research areas. Opinions on the appropriate positioning of social-ecological science in the LTER Network have varied over the past two decades. In current practice, social-ecological science is applied vigorously at urban and agricultural sites and opportunistically at suburban and more remote sites. In addition to informing

social science, other foci too have gained added prominence in recent years. One example – rapid evolution – is likely to play an important role as the Earth system continues to change in the coming decades.

2.3 Societal Impacts and Challenges

The return on NSF’s investment in long term research through the LTER program has been enormous – not only in terms of scientific discovery (Figure 2.3), but also in terms of training and mentorship of scientists, formal and informal STEM education, the creation of shared ecological knowledge with ecosystem managers, and other societal impacts of LTER research.

As LTER sites and the LTER Network matured, their value as magnets for inter- and transdisciplinary collaboration and training also became apparent. The wealth of data and site knowledge, as well as creative and knowledgeable colleagues, attracted scholars from geosciences, engineering, sociology, economics, humanities, and the arts, as well as from diverse areas of biology. Graduate students, postdocs and early-career faculty with ambitious research agendas requiring multidisciplinary teams became involved and have been raising the bar for both team science and reproducible research methods.

At the many sites where partnerships with land and water management personnel are well established, findings are quickly incorporated into management plans and policy decisions. In turn, management questions spark new science. This translation is particularly fluid at sites with Forest Service and Agricultural Research Service participation in the research effort, but examples abound of close connections with regional agencies, state agencies, and NGOs that have been cultivated over many years.

Core LTER grants can provide direct stipend support for a few graduate students and undergraduates at each site (Figure 2.4), but the number of students who benefit indirectly from LTER activities is far greater – whether they use LTER data to establish a reference standard, synthesize data collected from large-scale experiments, or participate in education and management partnerships that are nurtured by LTER personnel. Such interactions provide students with

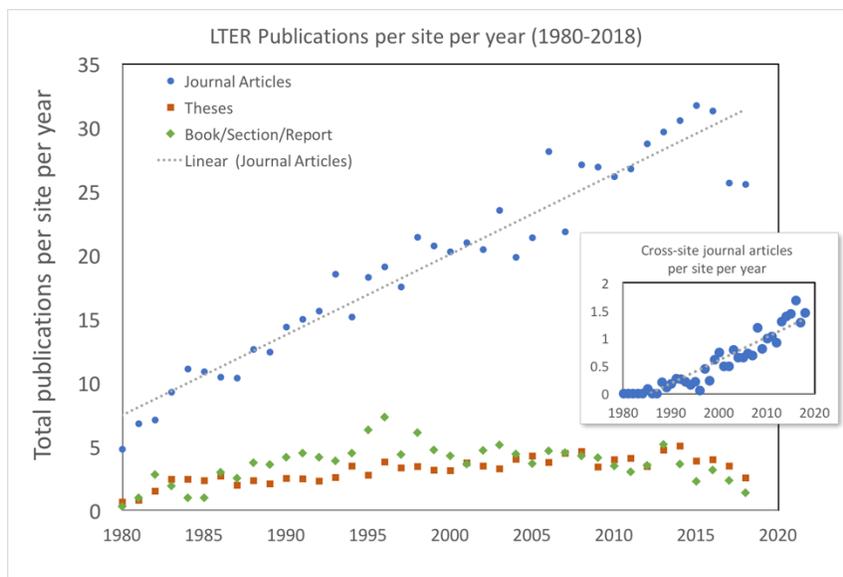


Figure 2.3. Number of LTER-related journal articles, books or book chapters, and theses produced per site per year. Inset depicts cross-site journal articles per site per year. Cross-site defined as those reported as a product by multiple sites. Publication database is available at: https://www.zotero.org/groups/2055673/lter_network/items

opportunities to engage with a network of over 6000 current and former LTER colleagues who are highly collaborative and almost universally happy to share their experience and connections.

One of the greatest challenges facing the LTER Network (and ecology and environmental science more broadly) over the next decade is to ensure the openness of that network to diverse participation at all levels. Work is underway on the simpler solutions (democratizing images and language, opening recruiting practices, making inclusivity resources available, developing and promoting codes of conduct), but introspection and cultural change are also required. The dominant culture of science can be a daunting obstacle for newcomers. Some aspects of this culture are necessarily challenging (mastery of a body of knowledge, quantitative and analytical skills, research at remote field stations); but other difficult aspects (poor work-life balance, narrow options for dress and forms of expression, assumptions of financial capacity) only serve to create unnecessary barriers to entry and advancement for individuals from underrepresented groups and those with caregiving obligations.

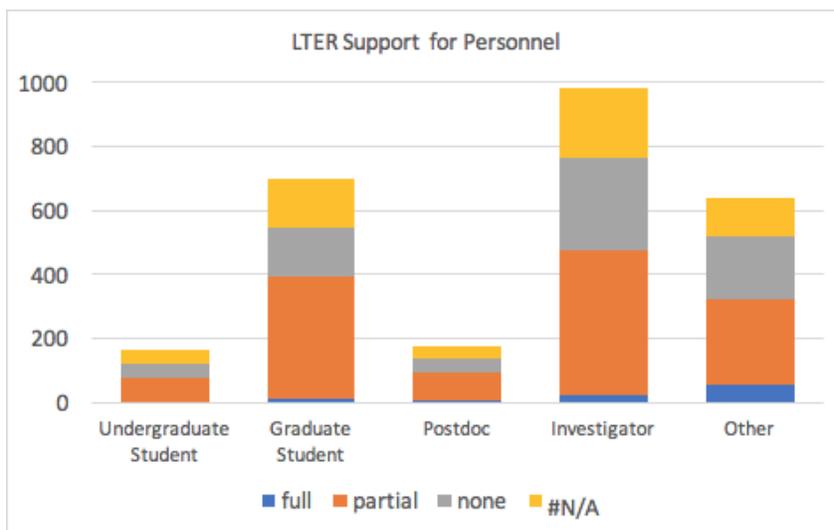
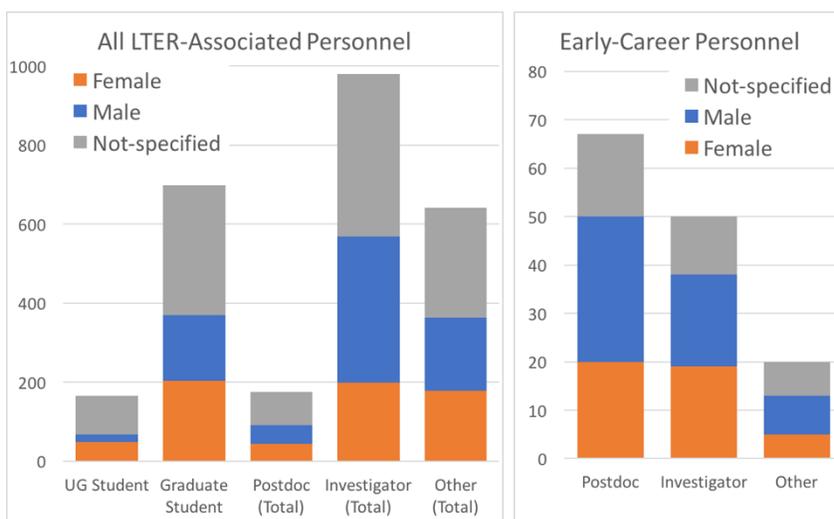


Figure 2.4. Top panel: level of support for LTER personnel in various roles. The vast majority of “LTER personnel” receive little or no support from LTER grants.

Bottom left panel: Gender distribution by role and career-stage. “Other” category includes information managers, education managers, other professionals and staff positions.

Bottom-right panel: Early-career responses are a subset of total responses for each career stage.



Current tracking of LTER demographics is inadequate to provide more complete demographic information, including on ethnic, racial, economic, or educational backgrounds. A new system is planned for implementation in 2019 that will allow direct responses from individuals to be maintained in a way that ensures information privacy.

The Network has a renewed sense of urgency to address these barriers. At the site level, honest conversations are taking place at executive team and all-hands meetings and websites, onboarding, and mentoring practices are changing; at the Network level, new partnerships are being established with national programs to support inclusion and effective mentoring and new administrative systems are being applied that will allow us to fine tune methods and document results (Figure 2.4).

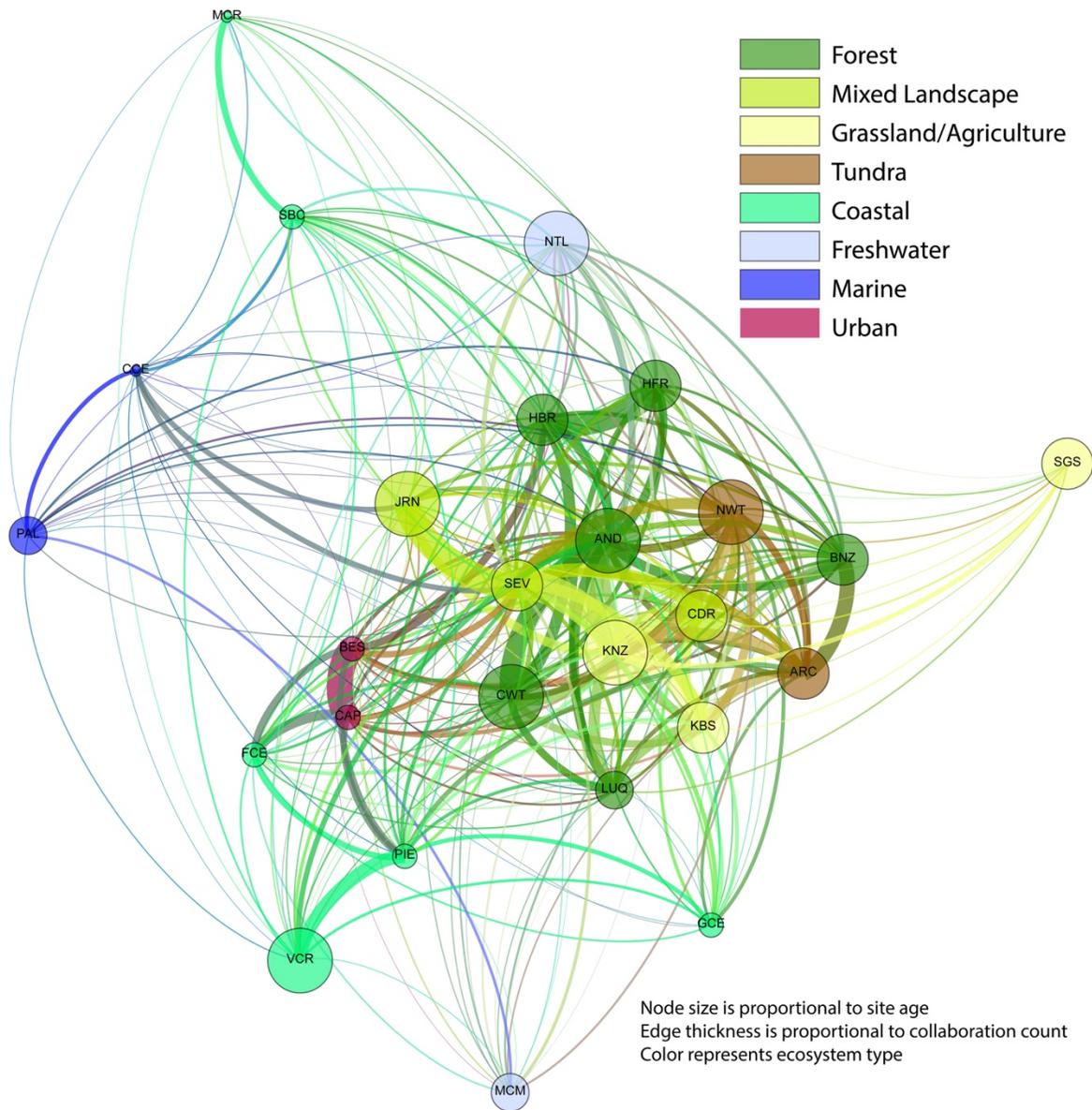


Figure 2.5. Network analysis of intra-LTER collaboration includes cross-site journal articles from 1981-2018. Node thickness represents count of cross-site journal articles. Node size represents duration of NSF funding for LTER site. Edge color is linked to connecting nodes. Visualization produced in Gephi 0.9.1 using force-matrix algorithm.

2.4 Change and Promise

The Network has seen and effectively managed considerable change. Principal investigators who have provided a steady hand for decades are retiring and new PIs are stepping up, bringing fresh perspectives and approaches. In the last 5 years, 14 of 25 continuing sites have welcomed a new Lead Principal Investigator. In 2016, NSF moved the Network Office from the University of New Mexico to the University of California, Santa Barbara and established the Environmental Data Initiative (EDI) as a separate data repository that efficiently collects and serves an immense variety of environmental data from a widely-distributed community of researchers. These changes have benefitted from and enhanced the emphasis on succession planning, diversity and inclusion, and documentation and sharing of best practices that support the long term health and vitality of the Network.

As we enter the 5th decade of the LTER program, the Network is stronger than ever. The recent increase in the number of coastal and ocean sites has broadened the representation of ecosystems in the LTER Network. New methods, such as genomics, high frequency sensors, autonomous observing vehicles, animal tracking technology, and new remote sensing technologies are allowing researchers to collect data at a pace and from locations and scales that previously were impractical or even impossible. Complementary Networks, such as NEON, CZO, the Global Lake Ecological Observatory Network (GLEON), and international LTER network (ILTER) create new opportunities to test at continental and global scales the principles that emerge from LTER inquiry. And the value of long term observations, experiments, and site based knowledge only grows with time.

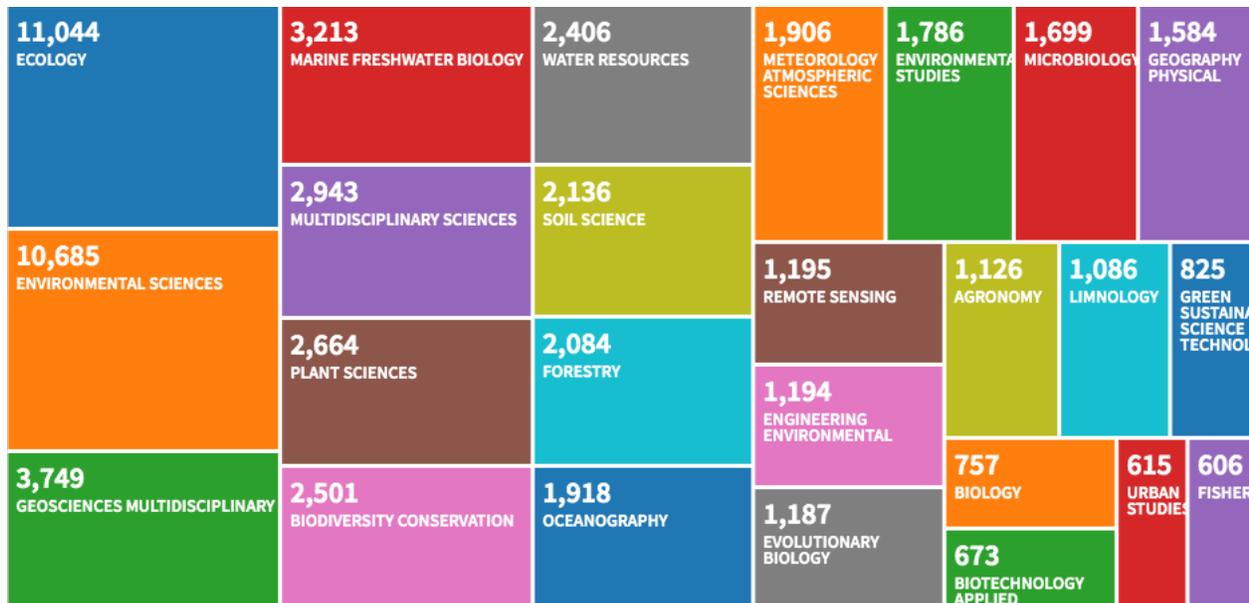


Figure 2.6. Primary research area (as identified by Web of Science) for articles citing 2009-2018 articles with LTER or “long-term ecological research” in the funding agency field and foreign funding agencies excluded (n=2207).

Convergence science thrives when a compelling place and problem attract a diversity of collaborators. LTER sites have been nucleating such alliances for decades and the expanded role of synthesis working groups, together with investments in environmental data science and cyberinfrastructure, are enabling even broader collaborations and applications, illustrated by the density of intra-network collaborations over the past 4 decades (Figure 2.5) and the diversity of research fields citing a representative subset of LTER research articles (Figure 2.6).

The LTER platform continues to attract graduate students and early career faculty with ambitious research agendas. Advances in LTER research over the past 10 years have improved our ability to make and test specific predictions about ecosystems and to work with managers to apply that knowledge for the benefit of humans and ecosystems.

As our nation and our world face unprecedented changes, sustaining ecosystem function and services will depend upon a clear understanding of the mechanisms that underlie ecosystem change, resilience, and recovery. The LTER Network — bursting with robust long term studies specifically designed to reveal the ecological mechanisms connecting drivers with outcomes — is uniquely able to advance that understanding.

3 Response to the 30-year Review

The review committee assembled by NSF to review the LTER Network at 30 years produced a report that was highly laudatory, noting that *“the Long-Term Ecological Research Program is one of the jewels in the NSF crown. No other program has had such a transformative role on the field of ecology as the LTER. Let there be no question – the LTER program has been an extraordinary success story within the National Science Foundation and one that, if funding continues at the same level, has the ability to produce as much or more in the coming decades.”*

The 30-year review team ended their report with a list of eight recommendations for the program. These recommendations were re-ordered and annotated by NSF program officers. The materials we have produced are based on the recommendations that constituted the NSF “response to the 30-year review.” Here, we review the list of recommendations and the progress we have made in addressing them over the last 10 years.

1. Resources are a key limiting factor for the future of the Network.

In the NSF response to the 30-year review, they note that “this recommendation sets the context within which all of the remaining recommendations must be evaluated. NSF considers it essential that LTER sites prioritize their research, data management, and education and outreach efforts.”

Over the past decade, we have prioritized using LTER funds for research, data management, and education and outreach efforts and successfully acquired non-LTER funds for new initiatives. For example, we devoted a series of annual Science Council meetings to reviewing the five core areas of LTER research and highlighting key areas of promising research that could only be addressed with long term data.

These meetings, and the triennial All Scientists’ Meetings were useful for developing collaborative research ideas that have seeded synthesis proposals and funding proposals to other NSF programs, other federal agencies, and private foundations. Based on reports from LTER sites of grants over \$25K, the LTER program brings in two dollars of outside support for each dollar invested by the NSF LTER programs (Figure 2.2). LTER sites have been especially competitive in Macrosystems Biology, Water Sustainability and Climate, Coastal Sustainability, Sustainability Research Network, Dynamics of Coupled Natural and Human Systems and Research Coordination Network programs.

At NSF’s encouragement following the 20-year review, the Network developed a decadal plan, a strategic plan, and a series of research prospectuses. At the time they were released (in the midst of an economic downturn and around the time of the 30-year review), those plans did not align with NSF’s funding priorities. However, the exercise of developing them highlighted many research ideas and collaborative activities that have since born fruit through crosscutting programs at NSF and other agencies.

2. Data management at each LTER site is adequate to excellent in its support of the current science questions at sites, but the LTER Network (1) must markedly expand its current data activities into a fully functional data management system that serves and archives all LTER data and metadata from all sites in a consistent and easily used manner to third-party users; (2) as a

whole must invest in making LTER data comparable across sites and more readily available to those interested in network-wide analyses.

As noted in section 13 information management in the LTER Network has long been a leading force in data archiving and publishing across NSF programs and has been “taken to the next level” in the last 10 years. The LTER data repository infrastructure (PASTA) has been in production since 2013 as part of the LTER Network Information System (NIS) (a node in DataONE) and LTER information managers have been involved in both the initial development and continued improvement of the Ecological Metadata Language (EML), a cornerstone of the priorities established by the Network long before the expression ‘FAIR data principles’ (Findable, Accessible, Interoperable, and Reusable) was coined. LTER data are **findable** (in the LTER data portal, DataONE and Google Dataset search) because they reside in an open repository, with unique and persistent identifiers and standard metadata indexed as a searchable resource. The data are **accessible** through industry standard protocols and are, in most cases, under an open-access license (access control is available if required). **Interoperability** is achieved by archiving data in commonly used file formats, and both metadata and data are machine readable and accessible. Rich, high quality science metadata in EML format render data fit for **reuse** in multiple contexts and environments, along with easily generated data provenance to document their lineage.

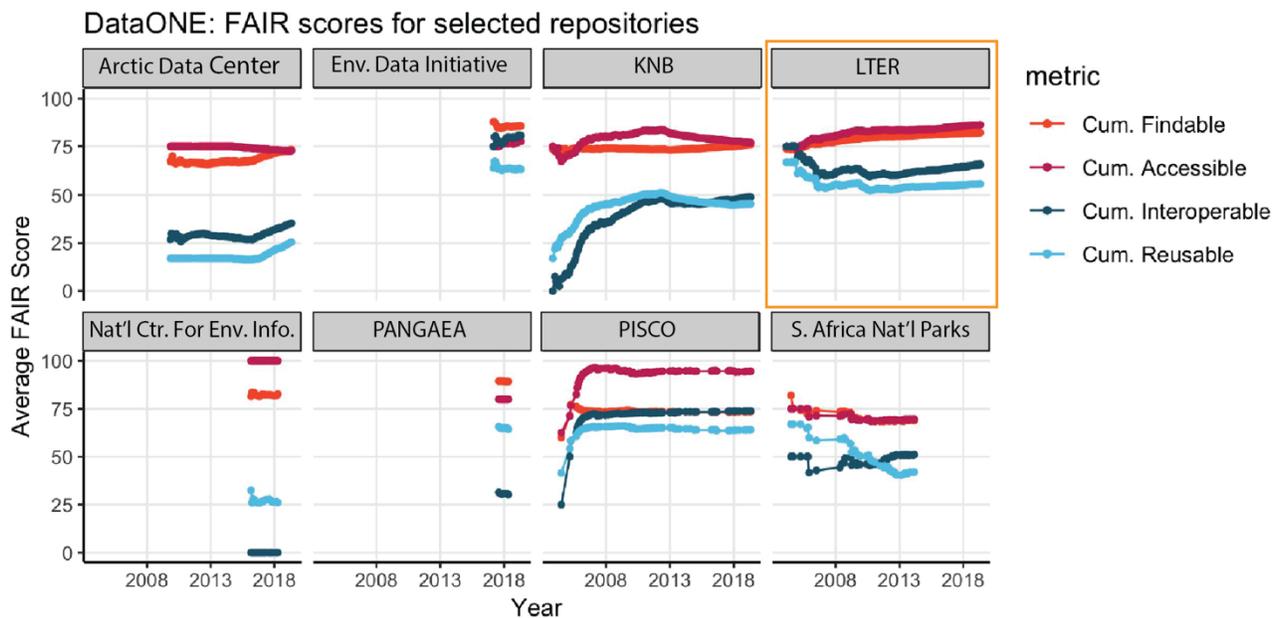


Figure 3.1. Change in FAIR scores of selected repositories over the past 15 years. From DataONE webinar, 05/14/2019.

A recent cross-repository analysis of FAIR metrics places LTER and EDI data on par with the best national and international repositories for findability and accessibility and better than most other repositories for interoperability and reusability³. This is a particularly notable accomplishment in light of the variety of data holdings in the LTER and EDI repository. Most recently, we are proud that the LTER approach to information management has been made available to a much wider community

through the Environmental Data Initiative repository (EDI), which was developed by LTER information managers and has LTER data and information management principles at its core.

3. *LTER must clearly articulate (a) what challenges long term data are uniquely poised to answer and (b) what the LTER Network can offer beyond a collection of excellent long term studies on diverse issues at ecologically distinctive sites.*

For this review, we have produced a series of synthetic narratives illustrating how LTER funding has facilitated unique and important scientific findings and societal impacts of broad relevance in ecology. Our objective has been to show how funding for long term research has allowed us to address the hardest and most important questions in ecology, such as anticipating ecosystem transitions, understanding the effects of resource variability, or identifying how evolutionary dynamics may mitigate or exacerbate the impacts of environmental change. The examples that we present highlight questions that require decades of long term data collection to address. They have emerged from both deliberate self-reflection^{4,5} and through facilitated serendipity, such as the annual Science Council meetings and the triennial All Scientists' Meetings. These narratives demonstrate that we are continuing to make fundamental basic science advances that are critical to addressing important environmental problems, and that provide a platform for effective education and engagement with stakeholders and other public audiences.

Throughout this document and in the site briefs that follow, we have included numerous examples of the translation and co-production of ecosystem management knowledge that is only possible because of the trusting relationships between LTER scientists and resource managers that have developed over years. A recent pilot grant to the Hubbard Brook and Harvard Forest sites is deliberately examining the nature of those relationships and what methods are most effective for establishing and maintaining them and a larger proposal is under development to expand the effort to multiple sites.

Long term relationships with educators are equally important. Modest "Schoolyard LTER" funding to sites is leveraged many-fold at most sites because of the stability it offers for maintaining connections to school systems, individual educators, and non-governmental and cultural organizations such as Mass Audubon (Plum Island Ecosystem LTER), Winter Wildlands Snow School (Niwot Ridge LTER), Asombro Institute for Education (Jornada LTER), and many others.

4. *Although all LTER sites should incorporate appropriate social-science data into their analyses, we are not convinced that social science research is, in its own right, a central value-added component for the Network as a whole, but it may well be so at some individual sites. Before undertaking a major network-wide expansion of social science research, the value of such an expansion must be better articulated and demonstrated.*

As recommended, there has been no network-wide expansion of social-ecological research, rather the LTER Network in 2020 exhibits a marked variation in the importance of social science research components. One of our synthetic narratives addresses research in coupled social-ecological systems and highlights important contributions from a significant subset of sites. While many of the examples come from the two urban sites and one cropland site, we note that social science data have produced important insights at sites across the Network, including Plum Island LTER, Florida Coastal Everglades LTER, as well as North Temperate Lakes and Coweeta LTERs, which received

“regionalization” funding supplements. Several cross-site projects centered on the interface between biophysical and social sciences and including different subsets of LTER sites have been funded through NSF cross-cutting programs and other agencies. These include Macrosystems Biology (urban homogenization); Coastal Sustainability (restoration and redevelopment at Baltimore LTER and sea-level rise and societal feedbacks at a consortium of East Coast LTER sites); Water, Sustainability and Climate (Yahara 2020 at the North Temperate Lakes LTER; robust decision making for South Florida); and the Urban Sustainability Research Network, which emerged from the Central-Arizona Phoenix LTER, and which is now developing an international face through NSF’s AccelNet program. Long term data streams provide novel insights into the relationships between ecosystems and complex social-ecological systems and LTER has made and continues to make novel and important contributions to sustainability science and convergence science.

5. *Recommendation: The richness of the long term observational data gathered across the LTER Network makes it uniquely and optimally poised to establish cross-site experimental studies of the mechanisms whereby factors such as climate change, nutrient loading, loss of biodiversity, shifts in species composition and food web structure, and invasive species impact ecosystem functioning and species dynamics. Although each site is likely suitable for only a subset of these experiments, the Network as a whole would add immeasurably to ecological science by pursuing such coordinated multi-site experimental studies. We recommend that the Network plan and actively seek funds for a coordinated program of cross-site experiments and related cross-site observations.*

NSF noted that while they are “enthusiastic about the development of more cross-site interactions ... it will be essential for LTER sites to seek financial support from diverse funding sources, both within and outside of the NSF.” And indeed, this is what we have done. Given a clear signal that we would need to seek funding for cross-site experimental studies outside of the LTER program, we have initiated multiple cross-site studies funded by the Macrosystems Biology; Water, Sustainability and Climate; Coastal Sustainability; Sustainability Research Network; Dynamics of Coupled Natural and Human Systems; and Research Coordination Network programs. Examples of these studies are highlighted in our synthetic research narratives and in the detailed description of “leveraged funding” elsewhere in this report.

An additional success has been the active participation and leadership of LTER sites in new grassroots distributed experiments and coordinated observation networks such as NutNet, DroughtNet, GLEON, Project Baseline and the National Phenology Network. Synthesis working groups organized through the Network Office and at other synthesis centers take full advantage of these networks to develop and test theory and scale local results. The approach is consistent with LTER’s bottom-up ethos and also helps motivate and incentivize data curation, archiving, and access.

6. *Recommendation: To ensure success, the LTER sites should actively recruit a new generation of diverse scholars interested in dedicating their careers to experimental and observational studies at the continental scale.*

As noted in the introduction to this report, LTER is in the midst of a generational turnover at the site and the network level. The transitions have caused few disruptions, as most sites have been preparing for this transition for some time and have been actively incorporating younger collaborators with

diverse perspectives. Planning for leadership transitions has been a formal discussion topic of least three recent Lead PI meetings. Synthesis activities supported by the LTER Network Offices have allowed potential new leaders to develop team science skills and strengthen connections between sites. Indeed, the turnover has created many new opportunities, increasing the proportion of female lead PI's from 25% to 40% over the past decade.

In addition, LTER scientists have held leadership roles in NutNet, DroughtNet, and GLEON and have recruited many sites into those networks that are led by more junior scientists who were not previously associated with LTER. Because of the modest initial investment required, this particular model of distributed observational networks has proved especially helpful in building on-the-ground international science networks.

The addition of new site leaders, new Network Office leadership, and three new sites in the past three years has motivated LTER to more clearly articulate governance practices (committee membership, annual committee reports, executive board bylaws and minutes) and further develop shared information resources (website and document archive; shared drives; community platform coming soon). These changes will continue to yield benefits for ease of operations, broader inclusion, improved communication, idea generation, and shared leadership.

The LTER Network faces many of the same challenges as the entire field of ecology when it comes to making the culture of STEM more broadly inclusive of differences in race, class, ethnicity, gender identity, and affectional preferences. The Network also has some unique assets that can make it a leader in this area. The 2018 All Scientists' Meeting included a cohort of 15 undergraduate researchers from diverse backgrounds who were deliberately recruited and received financial support to attend the meeting. All LTER undergraduate researchers were encouraged to participate in two pre-meeting webinars and all undergraduate ASM meeting participants were invited to join group activities. Surveyed undergraduates reported a universally positive experience built on a combination of cohort bonding, scientific challenge, and welcome into an extended family of researchers. Some significant portion of this group – and others from the 5 REU sites within the Network – will surely end up as long term investigators.

Recent investment by NSF and others has produced a wealth of resources and best practices on inclusive scientific culture. The LTER Network Office is sharing those resources with the Network and actively creating opportunities for discussion with PIs and Site Managers so that each site can incorporate the newest thinking into their own local context. However, progress in this area is particularly difficult to measure, as the data that NSF collects on participant demographics cannot be made available at the program level. The LTER Network Office is implementing a constituent relationship management system that will allow collection of demographic data with appropriate privacy controls and we look forward to developing a much clearer picture of our current status and progress over the coming decade.

7. Recommendation: Citizen science shows increasing promise as an outreach and educational tool to local communities and to audiences with a diversity that reflects the nation. Some LTER sites are encouraging this, among their other educational activities. These efforts should continue and be initiated at other sites. Their success is partially predicated on increasing the

diversity of scientists, staff and students at each site as role models to the citizen scientists and each site must enhance its efforts in this area.

Several LTER sites have robust and innovative programs that involve and inform their surrounding communities. At Bonanza Creek LTER, researchers work with native Alaskan subsistence hunters to understand how changing climate is affecting their access to food resources. Cedar Creek LTER has trained over 4700 individuals globally in crowdsourced image identification of wildlife, with the goal of understanding abundance, distribution, trophic cascades and spatial and temporal changes in wildlife communities. Many sites work with established citizen science projects such as the National Phenology Network; at least five sites are currently working on a pilot program aimed at adapting standardized protocols for an LTER Network initiative. Multiple sites are also working on joint data collection on soils and decomposition following standardized protocols. The Network endorses the value of civic science for its potential to build interest in STEM and to engage diverse communities, but a network-wide model seems to dilute the potential for sites to connect with *particular* communities.

8. Recommendation: Cross-site education programs should be a higher priority for funding and effort, both through the spread of the better program models and for education activities that truly leverage the Network as a whole. The few cross-site educational programs that have been offered to date have been very promising but funding has been minimal. It is critical to identify funding mechanisms for cross-site education both within and beyond NSF. Such programs should emphasize participation by diverse students and stakeholders.

The response by NSF to this recommendation noted that “Although NSF recognizes the promise of an expanded education and outreach effort across LTER sites, we emphasize the need for sites to prioritize their activities to fit within core LTER funding.” In fact, education and outreach programs have been extraordinarily successful at leveraging modest LTER seed funding through organizational partnerships and alternative funding sources. Multiple examples of such leveraging at particular sites can be found throughout the broader impacts sections of the site briefs that accompany this document. At the network level, they include a Math Science Partnership that expanded and connected data literacy programs, the launch of the UFERN research collaboration network to support evidence-based practices in undergraduate research experiences, funding for the LTER Schoolyard Book Series and for individual books in the series, and an Advancing Informal Science Learning project to understand what motivates participation in stakeholder engagement and what factors lead to successful engagement experiences.

The education programs at individual LTER sites are tailored to the science, communities, ecosystems, and partnerships where they are located and sites have to prioritize opportunities with the greatest promise of impact for their communities. The LTER Network maintains an active Education and Outreach Committee (EOC), which meets monthly to support mutual learning, coordinate activities, and share best practices and resources among sites. Subcommittees of the EOC focus on Data Literacy, REU and RET experiences, Citizen Science, the LTER Schoolyard Book Series, and other related topics as they arise. A shared Google Drive provides access to committee documents and allows coordinated activity planning.

At the network level, the greatest emphasis has been on programs that are common to most or all sites — or those where long term research has an especially important role to play. These include research experience for undergraduates and for teachers (REU/RET) programs, data literacy, and engagement with landowners, environmental planners and land and water management professionals. Additional detail on accomplishments and approaches to these focal areas can be found in the Education and Outreach Committee brief (Section 14) following the main body of the report.

9. Recommendation: As the goals and spread of long term science continue to broaden, it is becoming critical to think beyond networked LTER sites, towards networks of networks (including but not restricted to an LTER-NEON network). The LTER Network is uniquely poised to seek a leadership role in achieving this goal, and should articulate a concrete vision statement about its leadership opportunities. To ensure success, the LTER program should actively recruit a new generation of diverse scholars pursuing experimental and observational studies at the continental scale.

Over the past 10 years, interaction with NEON and other environmental monitoring and research networks, especially the Critical Zone Observatory (CZO) and International LTER (ILTER) networks, has been a major focus. The LTER Network has made a concerted effort to formalize interactions with NEON, CZO and ILTER. The Chair of the LTER Science Council (Groffman) served on the NEON Scientific and Technical Advisory Committee and the CZO Scientific Steering Committee. He also led a NEON Early Science Program project on “Synergies between LTER and NEON.” A series of manuscripts has highlighted the exciting scientific opportunities arising from networks of networks⁶⁻⁹.

In 2019, three members of the LTER Executive Board have each taken on the role of liaison with NEON, ILTER, or the Organization of Biological Field Stations (OBFS), helping to build more formal organizational ties. Joint symposia with NEON at several recent Ecological Society meetings have also helped build substantive connections and are gradually building recognition that LTER and NEON complement and build on each other’s strengths.

Some final thoughts:

Finally, we note that over the past decade the LTER Network has successfully responded to shifts in perspective and management structure on the part of NSF, as happened between the 20-year and 30-year reviews. In particular, for a number of LTER sites, new lead investigators have “taken up the baton” to carry the long term site research into the future. For example, the executive board of the LTER Network is now comprised of a majority of lead PIs in their first 6-year cycle. In the context of broader impacts, during the past decade the Network has leveraged the continuity of the LTER program to make substantial advancements that have gone beyond advancing ecosystem science and contributed to NSF’s broad goals, such as harnessing the data revolution (EDI and expanded synthesis activities) and broadening participation in STEM (e.g. LTER Schoolyard Book Series, data literacy, and REU mentoring). While we recognize that there will continue to be changes in NSF’s priorities given the long term nature of the LTER program, communication about changes in priorities and process will help to maintain the network’s productivity, creativity, and success in attracting new investigators in the coming decades.

Overall, there is a strong sense within the Network that our most important activity by far is to focus on the science that we do and use the resources we have (our long term data, our social and human capital, and our governance structure) to develop scientific ideas that can only be addressed through long term studies. Our experience over the past 10 years suggests that focusing on science and using our available resources efficiently positions us to take advantage of opportunities as they arise and will ensure that the LTER Network remains a novel and important “jewel in the NSF crown.”

4 LTER Science Advances: Selected Themes and Examples

Long term studies play a disproportionate role in advancing the field of ecology, none greater than those conducted at LTER sites¹⁰. In an era of rapid environmental change, the multi-decadal studies at LTER sites also help understand and predict local ecosystem responses to trends in air and water pollution, climate, invasive exotic species, and land use change. Thus, LTER science advances fundamental knowledge that is often of immediate relevance to environmental policy and management.

Take, for example, insights gained after 26 years in a soil warming experiment at Harvard Forest¹¹. The world's longest running soil warming experiment revealed surprising long-term cycles in soil carbon decay and associated microbial community response. Researchers discovered that a biological priming mechanism led to accelerated transfer of carbon from more recalcitrant to more easily metabolized forms of soil organic matter and created a feedback cycle that could greatly amplify the impact of warming on carbon transfer from the soil to the atmosphere in mid-latitude forests.

LTER site and cross-site studies have revealed important similarities and differences in how ecosystems respond to trends in environmental drivers such as climate. For instance, at LTER grassland sites, researchers have shown that net primary productivity (NPP) is highly sensitive not only to current-year climate but also to multi-year variability in climate, and that higher interannual rainfall variability may favor shrubs over grasses¹²⁻¹⁵. The important role of climate variability could only be revealed through long term research, and is now receiving increased attention as evidence mounts linking climate change to increasing interannual variation in precipitation.

The past decade of LTER science is replete with such influential studies and has produced thousands of research products. Rather than attempting a comprehensive review of this work, we synthesize research in eight thematic areas identified by site PIs in planning for the 2019 Science Council meeting as having broad importance across the LTER Network and where there have been especially significant research activity and gains over the past decade. The thematic areas include:

- [Nutrient supply effects on ecosystems](#)
- [Consumer controls on communities and ecosystems](#)
- [The role of historical legacies in today's ecosystems](#)
- [Biodiversity and ecosystem functioning](#)
- [Physical, chemical, and biological connectivity](#)
- [Coupled social-ecological systems](#)
- [Resistance, resilience & state change](#)
- [Evolution in ecological experiments](#)

For each theme, we summarize its general societal and scientific importance, provide a brief historical context for LTER research over the past decade, spotlight recent literature and specific research examples, and briefly touch on emerging directions and opportunities.

5 Nutrient Supply Effects on Ecosystems

Nutrient supply has long been recognized by ecologists as a key process structuring communities and ecosystems¹⁶⁻¹⁹, and manipulation of nutrient supply has always figured prominently in LTER experimental research. Interest in nutrient supply effects has not dimmed over time; rather, long term experiments continue to yield new insights and surprises. As discussed below, we now know that short term results can be misleading and that long term ecosystem responses to nutrient additions and reductions may not be symmetrical. The scale and scope of LTER nutrient research is such that results have directly influenced regional environmental policy and management.

Ecologists developed theory at the nexus of ecosystem and community ecology to explore ecological systems with explicit nutrient dynamics²⁰⁻²⁴. This research produced testable predictions of the effects of nutrient supply on community structure and productivity as well as the effects of community structure on cycling and pools of biologically limiting nutrients such as nitrogen and phosphorus. It also provided a unifying framework linking physiological, population, community, and ecosystem ecology that informed understanding of the implications of human alteration of the Earth's biogeochemical cycles.

This alteration is profound, as the supply to Earth's ecosystems of biologically limiting nutrients, such as nitrogen and phosphorus, is now many times what it was in pre-industrial times²⁵⁻²⁹. The impacts of these nutrients are complex, can take many decades to fully manifest³⁰⁻³³, and result in declines in air and water quality, climate change, and biodiversity^{34,35}.

The inception of the LTER program corresponded with a rapid increase in the rate of nutrient loading from human sources and the development of theory linking nutrient cycling and community dynamics. As a result, studies on the effects of limiting nutrients in many different ecosystems played a large role in early LTER research programs, and these LTER experiments continue to be some of the longest running nutrient-addition experiments worldwide³⁶⁻⁴⁰. Across diverse sites from arctic and alpine tundra to grasslands, forests, streams, wetlands, and lakes, these experiments demonstrated the important role of nutrient supply in structuring communities and food webs⁴¹⁻⁴⁶, inducing losses of diversity^{42,43,46}, altering ecosystem productivity and carbon cycling^{31,37,47,48}, and even altering geomorphology and the movement of physical materials⁴⁹.

In addition to nutrient addition experiments, the long term data collected at LTER sites have been critical to detecting and understanding the impacts of increased nutrient loading on terrestrial and aquatic ecosystems^{33,50,51}. For example, intensive management of agricultural lands has resulted in high rates of nutrient loading to aquatic ecosystems^{25,51,52}. Long term measurements have allowed researchers to observe and understand myriad ecological changes associated with aquatic eutrophication and increasingly, to understand the interactions between these nutrient-driven water quality issues and changes in climate and community composition^{51,53}.

Long term observations and experiments at LTER sites have shown that short term patterns may have little bearing on the ultimate direction and magnitude of nutrient effects, which can play out over many decades^{30,37,38,49}. For example, long term (40-year) studies in the California Current Ecosystem LTER have revealed seasonal patterns in diatom iron deficiency with greater deficiencies in the spring and summer. Over the past 25 years, diatom iron deficiency has increased in ways that appear to be related to regional climate and patterns of upwelling⁵⁴.

Long term observations from the North Temperate Lakes LTER were critical for demonstrating the challenges and consequences of eutrophication in Lake Mendota, Wisconsin. Management efforts to improve water quality have been negated by an increasing frequency and intensity of storms that drive phosphorus to the lake⁵¹ and by the arrival of an invasive invertebrate predator (the spiny water flea) that has disrupted the food web and reduced top-down control of algal populations^{55,56}.

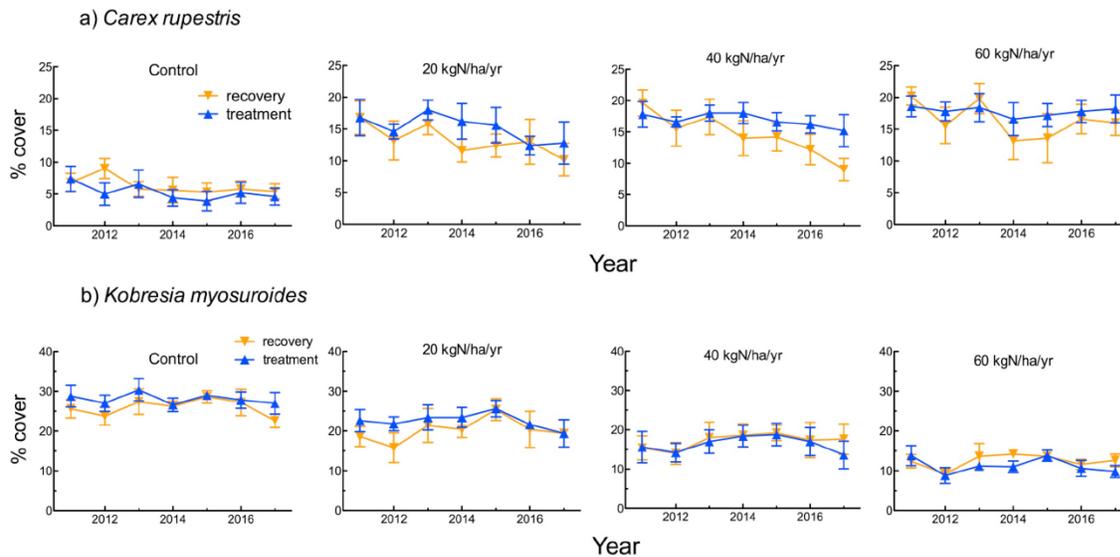


Figure 5.1. Projected cover of a nitrophilic species *Carex rupestris* (a) and the dominant sedge of a dry meadow community *Kobresia myosuroides* (b) in dry meadow plots at Niwot receiving different levels of nitrogen (M) since 1997 (blue symbols) and plots that received the same dosage between 1997 and 2008, but then received no treatment since 2009 (recovery, orange symbols). Symbols are means ($n = 5$), error bars show \pm SE. From Bowman et al. 2018.

Long term experiments have revealed unexpected dynamics. For example, in alpine tundra at Niwot LTER, nutrient addition shifted plant community composition in just four years, but after nutrient addition ceased in a subset of plots, plant community composition mirrored that of plots where nutrient addition continued for another eight years (Fig. 1)⁴⁶. Lack of recovery in the plant community was mirrored by lack of recovery in base cation concentrations, pH, and aluminum in nitrogen cessation plots. Similar lack of recovery following cessation of nitrogen inputs has been observed in long term studies at Cedar Creek LTER⁵⁷. More generally, these studies have yielded the hypothesis that nutrient-driven changes in plant composition may lead to alternate stable states in community structure and nutrient cycling³⁶.

Over time, nutrient effects can be mediated by interactions with geomorphological processes^{33,49}. For example, during the first years of a nutrient addition experiment in tidal creeks at Plum Island Ecosystems LTER, benthic algae, invertebrate prey, and a small fish, the mummichog (*Fundulus heteroclitus*) showed a classic bottom-up positive response to added nutrients. However, after six years creek banks began to collapse, likely due to decreased density of bank-stabilizing root biomass that altered creek geomorphology (Fig. 2)⁴⁹. This geomorphic change coincided with a decrease in

mummichog abundance in fertilized creeks and a much higher incidence of trematode parasites in amphipods^{49,58}.

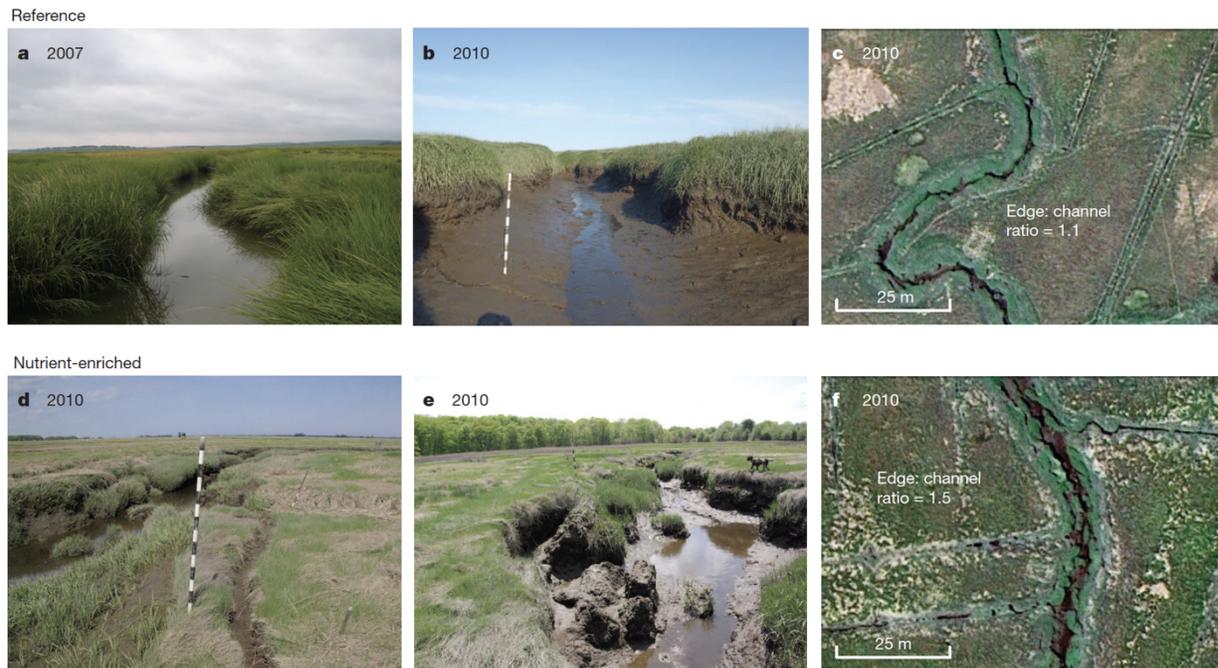


Figure 5.2. Comparison photos of the marshes from a nine-year ecosystem nutrient-enrichment experiment initiated in 2004. a–c, Reference. d–f, Nutrient-enriched. From Deegan et al. 2012.

Long term studies in coastal wetlands at the Florida Coastal Ecosystems LTER have demonstrated that seagrass beds and mangrove forests containing globally significant carbon stocks^{59,60} are vulnerable to saltwater intrusion driven by accelerating sea level rise^{61,62}. However, climate-driven coastal disturbances like tropical storms and floods also can deliver nutrients and inorganic materials to these ecosystems⁶³. These additions can offset the effects of rising seas by increasing coastal ecosystem productivity (Figure 5.3)^{62,64} and the accretion of organic and mineral soils⁶⁵. However, more freshwater delivery is needed to offset rapid soil loss in freshwater marshes exposed to saltwater intrusion⁶⁶.

LTER experiments and studies have expanded over time to examine nutrient limitation in tundra, grasslands, forests, coral reefs, lakes, wetlands, streams, and marine ecosystems^{36–40,49,54,67}. In addition, LTER research has expanded to, demonstrate that resource co-limitation is more common than previously appreciated^{45,47,54,67–71}, as predicted by theory^{47,70}, and that nutrient enrichment can have cascading effects on higher trophic levels^{39,49,72,73}. Finally, there has been a new focus on recovery of ecosystems from chronic nutrient addition through the use of nutrient cessation experiments e.g., the experiments at Niwot Ridge, Harvard Forest and Cedar Creek LTERs mentioned above.

Meta-analyses and distributed experiments motivated by LTER experiments have been used to test the generality of results and theory developed by LTER scientists^{42,71,74,75}. Meta-analyses of the effects of resources on ecosystems and communities have shown that rare species and certain

types of species such as nitrogen-fixers and natives are at greater risk for nutrient-induced extinction and that different kinds of ecosystems show different patterns of response (e.g., stepped versus directional) to resource enrichment^{38,42}. In the past decade, LTER meta-analyses have inspired standardized nutrient addition experiments across eight of the terrestrial LTER sites and over 100 grassland sites globally through the Nutrient Network (NutNet) project⁷⁴. This distributed experiment built off a history of standardized experiments in the LTER program (especially LIDET, a standardized, inter-site decomposition experiment that ran from 1990-2007)⁷⁶. This coordinated approach avoids some of the pitfalls of meta-analytical approaches in which each experiment uses different methods^{42,74}. The NutNet project has shown that most grassland sites are limited by multiple types of nutrients⁶⁹, and that increased nutrient supplies are expected to lead to declines in native diversity, increased invasions of exotic plants, and increased soil carbon storage^{70,71,77,78}. This work demonstrates the generality of the insights from theory and data originating at LTER sites.

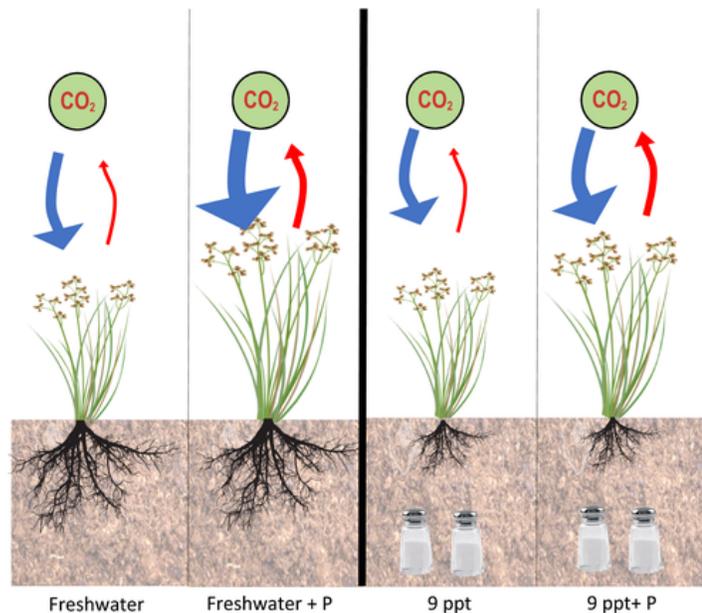


Figure 5.3. Conceptual summarization of how a freshwater, karstic wetland responds to saltwater intrusion given elevated salinity and a higher P load. Responses include changes in carbon dioxide (CO₂) cycling and aboveground and belowground vegetation. The flux arrows are drawn to scale based on the results in Wilson et al 2019. The responses of above and belowground vegetation are not drawn to scale but are representative the study results.

Nutrient research in the LTER Network has had significant impact on policy and practice. LTER research and scientists have provided important guidance for managing delivery of nutrients to coastal waters through the development of total maximum daily load regulations⁷⁹, informed EPA's protective water quality criteria for wetlands⁸⁰, enhanced protection of biodiversity through the development of critical load regulations⁴⁶, and improved of agricultural practices through changes in fertilizer practices⁸¹.

Most ecosystems are receiving increased loads of a variety of potentially biologically-limiting elemental nutrients, and there is widespread evidence that most ecosystems are synergistically limited by multiple nutrients (e.g., ^{69,70,75}). Nevertheless, most ecological research focuses on the effects of single nutrients which have historically been seen as the dominant limiting nutrient. Understanding the effects of nutrient enrichment requires ecologists to move beyond a single listing nutrient paradigm. Factorial nutrient additions at LTER sites and distributed experiment networks are primed to provide the needed information.

A key emerging issue is the effect of long term nutrient enrichment in altering ecosystem response to rising concentrations of atmospheric CO₂ and how that effect is represented in Earth System Models⁸² (Luo et al. 2004).

6 Consumer Controls on Communities and Ecosystems

Over 40 years ago, classic studies showed that consumers are important “top down” actors that also impact species distribution and abundance⁸³⁻⁸⁵. Much of today’s research into the role of consumers is driven by the growing realization that consumers drive both top down and bottom up ecosystem processes through complex pathways that were previously unimaginable, and by the recognition that consumers of all types are facing drastic declines globally.

Previous research at LTER sites has been influential in understanding how consumers: (1) impact species diversity and ecosystem function⁸⁶, (2) impact primary productivity⁸⁷, and (3) control the resilience of communities and influence ecosystem transitions⁸⁸. The examples below highlight recent insights from long term and experimental studies of consumers and trophic dynamics. These and other results from across the Network are already informing conservation and management.

In tallgrass prairie, the Konza LTER has maintained a 30+ year experiment examining the interactive impact of bison grazing and fire on plant community structure and ecosystem processes. The long study duration has enabled researchers to investigate consumer effects over multiple fire cycles ranging from 1- to 20-year return intervals, and across significant multi-year variation in climate. It is

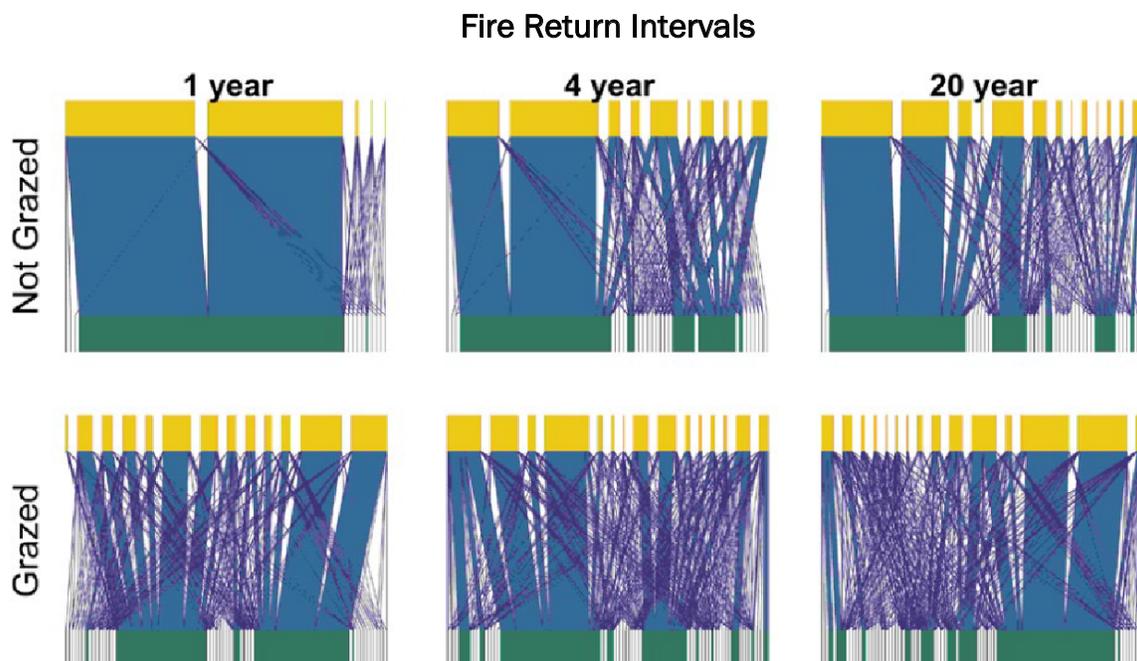


Figure 6.1. Comparison of representative plant–grasshopper networks from the Konza Prairie LTER. The top yellow bars represent grasshopper species, and the bottom green bars represent plant species in the network. The blue lines connecting plant and grasshopper species represent feeding links, and the thickness of the lines corresponds to the strength of the species’ interaction. Network panels are arranged by treatment with row indicating grazing treatment and columns indicating fire return interval. The annually burned and not grazed watershed in the top left is dominated by two grasshopper species (*Orphulella speciosa* and *Phoetaliotes nebrascensis*) and one plant species (*Andropogon gerardii*), whereas other fire and grazing treatments resulted in more complex grasshopper–plant networks. From Welti et al (2018).

now clear that bison combine with fire to create a mosaic of forage quality and quantity across the landscape⁸⁹. Grazing-induced changes in species assemblages and tissue quality affect canopy nitrogen availability and grassland heterogeneity⁹⁰. Grazing by bison alters root depth distribution and the water use of grassland plants, which in turn alters competitive interactions among grasses, forbs and shrubs⁹¹. Bison may also facilitate the expansion of woody vegetation by removing grass fuel loads, resulting in fires that are not intense enough to suppress woody vegetation⁹². Importantly, once these areas become dominated by woody vegetation, they appear resistant to fire, suppressing the return to grasslands⁹².

Bison also have important top-down impacts on plant insect interactions. Using a 19-year data set of plant and grasshopper abundance, Welty et al.⁹³ used DNA metabarcoding to examine how bison grazing, fire frequency, and climate impacted the diets of 26 grasshopper species. By constructing networks of plant-grasshopper interactions based off DNA sequences in the grasshopper digestive tract, they showed that the networks of plant-herbivore interactions in watersheds where bison were present were much more complex than the networks in watersheds where bison were absent. The grasshoppers were more diverse in areas grazed by bison and consumed a wider variety of species in the presence of bison, likely because bison grazing facilitates plant diversity, as other long term experiments at Konza Prairie have shown⁹⁴. Thus, the presence of a large herbivore changes the dynamics of plant communities and, in turn, the diet breadth of a smaller herbivores that feed on these plants.

In Alaska's boreal forest, herbivore interactions take a different turn. At the Bonanza Creek LTER, snowshoe hares — which experience decadal population cycles — are particularly important herbivores for shaping forest dynamics. During periods of high hare density, browsing on spruce seedlings can thin an entire spruce cohort, with results that persist for decades^{95,96}. Using a 40-year dataset, Bonanza Creek researchers showed that this 'snowshoe hare filter' impacts the establishment of white spruce⁹⁷. Although white spruce is expanding in elevation as the climate warms, snowshoe hares slow the rate of spruce establishment. Importantly, a shorter study would likely have missed this effect because hare abundance cycles so dramatically^{98,99} (Krebs et al. 2013, Krebs et al. 2014).

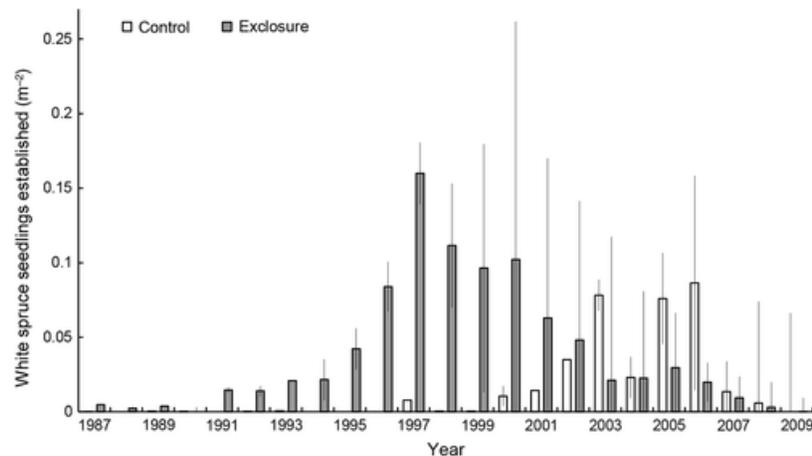


Figure 6.2. Pattern of yearly establishment for white spruce (seedlings established/m²) within naturally regenerating exclosure plots (gray bars) and control plots (white bars) at Bonanza Creek LTER along the Tanana River flood plain in Alaska, Mean ± SE, n = 7. From Olnes and Kielland (2016).

The role of lynx in this system underscores the importance of predation, which is strongly influenced by habitat, season, and body condition. By contrast, the population abundance of lynx, and therefore

likely their impact on hares and, in turn, the impact of hares on plants, is largely controlled by emigration and immigration as these predators move through the landscape in search of prey^{100,101}. Capturing these intriguing dynamics of large herbivores on ecosystems is often only possible with decades-long data sets on organismal abundance and landscape-scale manipulations of large herbivore abundance.

In addition to their effect on community dynamics and ecosystem function via predation and herbivory, consumers are also important recyclers and transporters of nutrients. Nutrients that are moved or mobilized by consumers can alter primary production and other key ecosystem processes. Research from the Florida Coastal Everglades (FCE) LTER has shown that large, dominant

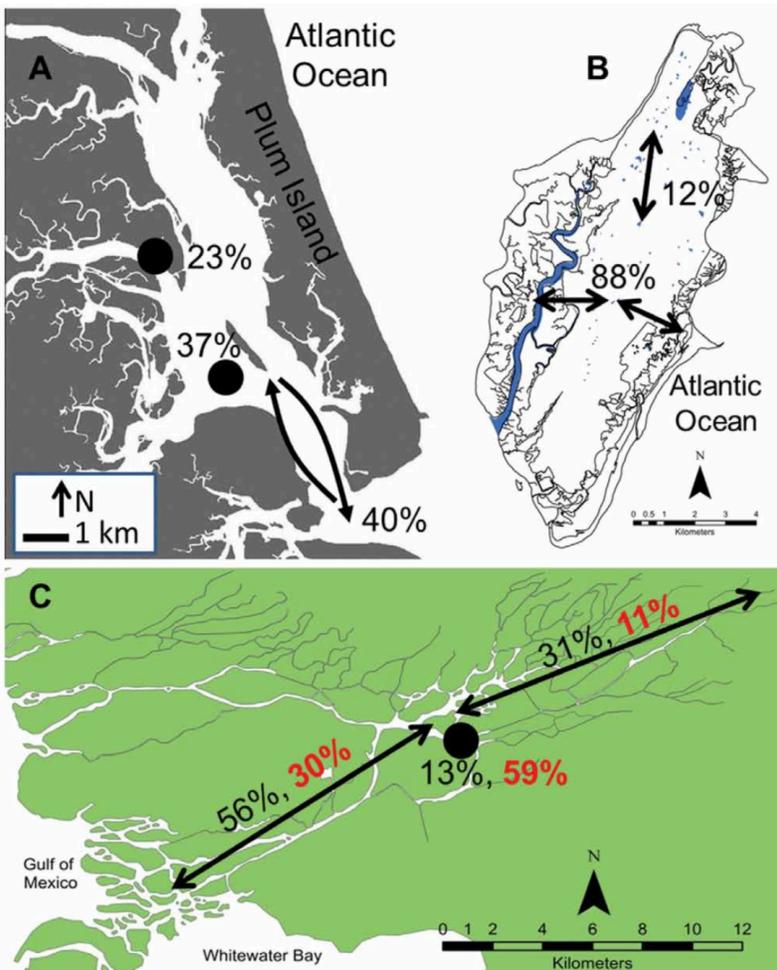


Figure 6.3. Detail maps of three LTER sites illustrating the variable movement patterns of large top predators. (a) Plum Island Estuary, MA. Dots represent locations where different striped bass (*Morone saxatilis*) foraging contingents remain during the feeding season, and arrows represent the foraging contingent that enters and then leaves the estuary. (b) Sapelo Island, GA arrows represent different groups of American alligators (*Alligator mississippiensis*) that either only move between different upland ponds/marshes or move between upland ponds/marshes and estuaries/marine habitats. (c) Shark River Estuary, FL, in the coastal Everglades. The dot represents an estuarine area where certain alligators and bull sharks (*Carcharhinus leucas*) remain resident year-round, and arrows represent other groups of alligators and bull sharks that either move between estuarine and marine habitats or between estuarine and freshwater habitats. In all maps, numbers indicate the percentage of the top predator population that exhibits each type of movement/habitat use behavior. In (c), black numbers correspond to alligators and red numbers correspond to bull sharks. From Rosenblatt et al (2013).

consumers such as American alligators, bull sharks, and common snook are important mobile links between freshwater and marine ecosystems¹⁰². Using acoustic telemetry, researchers at FCE showed that alligators frequently travel over 30 km from freshwater/estuarine habitats downstream to marine habitats to feed (Fig. 2)¹⁰², while juvenile bull sharks and snook make repeated seasonal movements upstream in estuarine habitats to forage on prey pulses originating from drying marshes^{103,104}.

Similarly, in the Georgia Coastal Ecosystem (GCE) LTER, almost 90% of the alligators move between freshwater ponds/marshes and estuarine/marine habitats (Fig 2)¹⁰⁵. An average adult alligator excretes upwards of 0.5 kg of P per day¹⁰⁶, and given that these freshwater systems are often phosphorus-limited, the transfer of marine-derived nutrients to freshwater habitats by these predators likely impacts primary production and community dynamics. Similar dynamics exist where movement of mobile predators transfers nutrients among marine ecosystems. A six-year tracking study at Plum Island Ecosystem (PIE) LTER showed that striped bass migrated out of this ecosystem in the fall, often moving hundreds of kilometers to other estuaries¹⁰⁷, with two-thirds of the fishes returning to PIE the next spring. Thus, striped bass can act as vectors of nutrients and energy, subsidizing other estuaries along the Atlantic Coast.

Research on the role of consumers in ecosystems in the LTER Network has significant broader impacts given that consumers are heavily exploited across most ecosystems on Earth^{108,109}. LTER research has shown that exploitation of herbivorous fishes and alterations to fishing behavior can impact — and are impacted by — community dynamics on coral reefs¹¹⁰. Other recent work has shown that alterations of fish communities have strong feedbacks on water quality in temperate eutrophic lakes¹¹¹, potentially changing long term patterns of eutrophication. Further, LTER research suggests that the abundance of both herbivores and predators impacts the amount of carbon primary producers sequester, thereby potentially affecting the global carbon cycle^{59,112}. Ultimately, the interaction of climate change, consumers, and ecosystem dynamics is building to be a strong area of research for the next decade of the LTER Network.

The major forces of global change, such as climate change, nutrient pollution, and overexploitation, do not act in isolation to impact ecosystems. These global change drivers often act synergistically to impact plant and animal populations and ecosystem processes. But these effects often take years or decades to manifest at the ecosystem level, timescales that are not captured by typical short term experiments or the average span of a grant cycle. Long term research is critical to understanding the impacts of these large scale drivers and the non-linearities and thresholds with which they operate.

7 The Role of Historical Legacies in Today's Ecosystems

LTER sites have played a key role in revealing how past events can exert a controlling influence on current and future ecosystem structure and function. The importance of legacies is not a novel observation, but can be difficult to quantify and to incorporate in short term studies. Glaciation, past land use, accumulated atmospheric pollution, and changes in grazing patterns or fire regime all create ecological legacies that influence how an ecosystem may develop or respond to perturbation in the present. The body of LTER work in this area includes several key long term observational data sets, experiments at multiple sites, the development of new theory, predictive modeling and significant broader impacts on international, national, and regional environmental policy, natural resource management, conservation and land planning, and habitat restoration.

Legacies, especially of past land use, were prominent at several LTER sites as they were being established. For example, the Harvard Forest and Jornada sites were established on lands that had been strongly affected by previous agricultural land use: cropping and pastures at Harvard Forest¹¹³ and grazing at Jornada¹¹⁴. At other sites, e.g., Luquillo, the effects of past land use became obvious only after LTER programs began to apply remote sensing and historical fieldwork and establish long term monitoring plots and experiments^{115,116}. Such studies provided clear demonstrations that events that occurred long in the past had strong and complex influences on current ecosystem structure, function, and services. Long term research on legacies has proven to be fundamental in several of the most challenging research areas of ecology including analysis of state changes and resilience^{117,118}, and factors controlling the spatial and temporal patterns of biodiversity and exotic species invasion. Recognition of the importance of legacies in these areas was greatly facilitated by, and would likely not have emerged without, the long term observations and experiments at LTER sites.

The scope of research on ecological legacies in the LTER Network expanded further into biogeochemistry with work at the Hubbard Brook site as investigators began to evaluate ecosystem recovery from decades of acid deposition (Figure 7.1) and realized that this recovery was greatly delayed due to a legacy of soil depletion of available base cations^{50,119}. Acid deposition accelerates leaching of base cations from soil pools that are important regulators of ecosystem productivity, decomposition, biodiversity, and response to disturbance. These observations led to a watershed-scale experiment which showed that calcium additions alleviated this legacy effect, reversed forest decline (Figure 7.2),

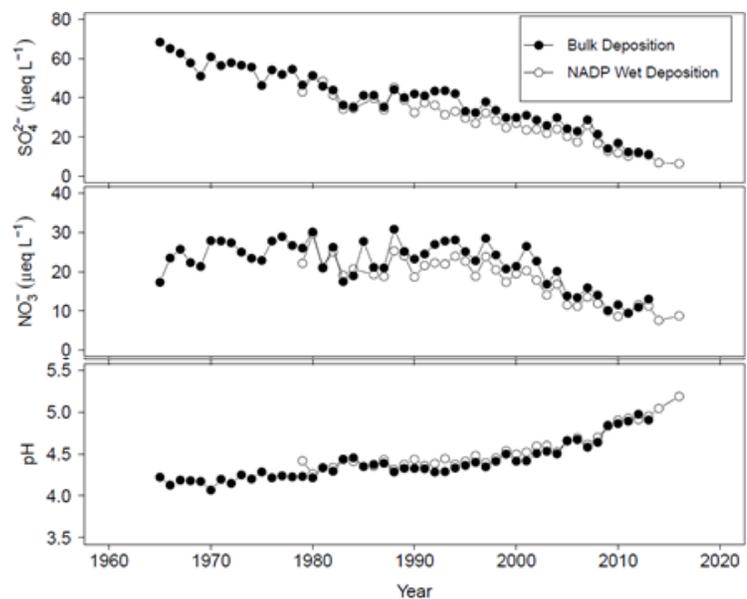


Figure 7.1. Long-term data from the Hubbard Brook LTER show that acid deposition is declining ... but it has left a long-term legacy in the soil: accumulation of sulfur and nitrogen and loss of base cations. Bulk deposition data available at: [doi:10.6073/pasta/573d0e1eb5d1ca541005f58146b95d19](https://doi.org/10.6073/pasta/573d0e1eb5d1ca541005f58146b95d19). Wet deposition data at: <http://nadp.slh.wisc.edu/data/ntr/>

improved health and reproduction of sugar maple, and improved the health of red spruce. But surprisingly it also increased litter decomposition, decreased soil carbon, and increased nitrate levels in streams. This experiment has raised new questions about ecosystem “deacidification”¹²⁰, which is occurring in many regions of the world, and is resulting in complex effects on carbon and nitrogen dynamics¹²¹.

At the H.J. Andrews Experimental Forest of Oregon, long term data show how export of dissolved organic carbon (DOC) is related to legacies of wood on the forest floor three to five decades after harvest of old-growth forest¹²². Reference watersheds with 150 to 500-year old Douglas fir/western hemlock forests and high biomass of logs on the forest floor had much higher DOC export than Douglas fir plantations established after clearcutting of old growth forest in the mid 1960s to mid 1970s (Figure 7.3). These legacies are likely to persist as total ecosystem carbon stocks, especially coarse woody debris, may require centuries to develop after old-growth forest harvest.

Long term analysis of legacies has raised new questions that can only be addressed with further long term research. Here we highlight two: 1) changes in fire frequency in the Arctic and 2) the role of sediment legacies in eutrophication in lakes.

Research at the Bonanza Creek LTER site is addressing the creation of new legacies through changes in fire regime which result in northern ecosystems becoming more vulnerable to regime shifts, including permafrost thaw and altered vegetation succession. Severe fires, which have been increasing in late summer, burn through and eliminate surface organic soil horizons, leaving mineral soils at the surface where plants colonize. The loss of surface organic soil favors the establishment of hardwoods over conifers. As a result, after severe fires, deciduous tree species such as aspen and birch establish at high densities. Predictions are that a substantial component of the landscape, which is currently dominated by black spruce, could be converted to hardwoods over the next 50-100 years.

Once deciduous forests are established, a new domain of feedbacks will emerge where rapidly decomposing litter from a broadleaf canopy maintains shallow organic soils. Deciduous broadleaf trees also increase rates of evapotranspiration and export of moisture from soil to the atmosphere. Once thick organic layers are consumed by fire, permafrost degradation is likely, leading to a state

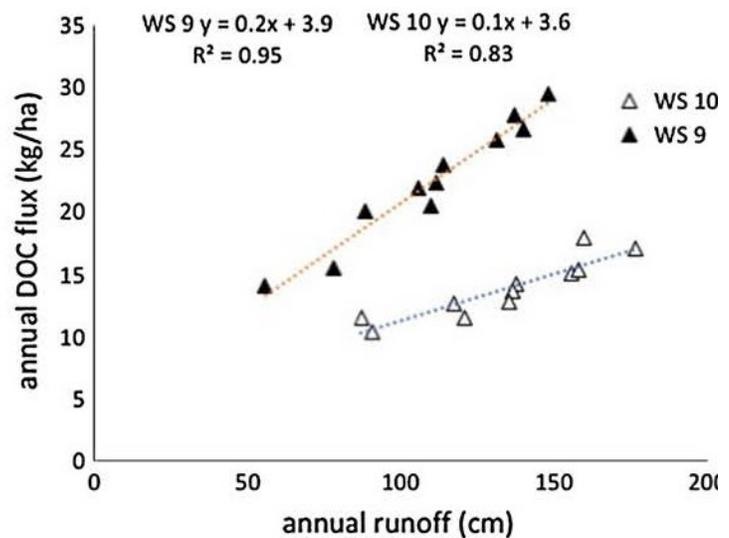


Figure 7.3. Annual dissolved organic carbon (DOC) flux (kg/ha) as a function of annual runoff (cm) for water years 2004 through 2014 (Oct to Sep) in two watersheds in the HJ Andrews Experimental Forest, Oregon. WS 9 is a reference watershed with 150 to 500-year old Douglas-fir/western hemlock forests and high biomass of logs on the forest floor had much higher DOC export than Douglas fir plantations established after clearcutting of old growth forest in the mid 1960s to mid 1970s.

change that permanently alters ecosystem structure and function, including ecosystem productivity and C storage¹²³, feedbacks to regional climate, and the availability of ecosystem services to society^{124,125}. This conversion will be very slow to reverse as organic horizons develop slowly over decades to centuries. This research demonstrates how the concept of legacies is allowing scientists to frame predictions about the long term effects of changing environmental conditions.



Figure 7.4. Creating new legacies through changes in fire regime. Research at the Bonanza Creek boreal LTER site shows that high severity fires burning through organic horizons to mineral soil favor the establishment of hardwoods over conifers. Predictions are that a substantial component of the black spruce landscape could be converted to hardwoods over the next 50-100 years.

Ongoing research at the North Temperate Lakes LTER site shows how sediment legacies underlie regime shifts – large, persistent, and often abrupt changes in ecosystem structure and function that may be difficult to reverse. Regime shifts are often precipitated by gradual changes in an underlying “big slow” variable such as soil or sediment nutrient stocks^{126,127}. In lakes, gradual increases in sediment phosphorus pools, generally associated with agricultural and urban land uses, increase susceptibility to a eutrophic condition. Once a lake becomes eutrophic, the legacy phosphorus in the sediments makes a return to normal water quality difficult¹²⁸. This effect creates great challenges for lake management; reduction of phosphorus inputs to the lakes produces little or no improvement in water quality because they are overwhelmed by the mass of legacy phosphorus that continues to be released from the lake sediments. These realities have motivated research on predicting regime shifts using high resolution sensors and advanced models¹²⁶, which would improve our ability to predict and manage lake systems in the context of persistent legacies.

An area of critical importance – which was initiated in 1988 with a simulated blowdown experiment at Harvard Forest¹²⁹ – is research into hurricanes and the diverse and complex legacies they create. Recent work at Florida Coastal Everglades LTER has characterized how sediment deposition associated with hurricanes has long term effects on nutrient dynamics in the Everglades^{64,130}. At Luquillo LTER, repeated hurricanes produce legacy effects on canopy structure and plant community composition¹³¹ and canopy trimming experiments allow comparison of different simulated return times. Here, long term monitoring and a strong understanding of legacy effects leaves the LTER Network poised to evaluate long term effects of anticipated changes in the frequency and/or intensity of major disturbance events¹³².

Both of these examples capitalize on observational studies, but experimental manipulation of disturbance can also be used to test for legacy effects. For example, nitrogen additions have ceased at long term plots at the Cedar Creek, Harvard Forest and Konza Prairie sites, allowing for evaluation of legacy and recovery. These examples highlight several ways that LTER science works that shorter term studies cannot: 1) Using long term monitoring to study legacy effects (Bonanza Creek and North Temperate Lakes), 2) Using long term experiments to create potential legacy-causing environmental changes in a replicated, experimental manner (Cedar Creek, Harvard Forest, and Konza Prairie), and 3) Using experiments to understand the causes of legacy effects (the Hubbard Brook acidification example in the first part of this vignette).

Research on ecological legacies bears directly on many environmental management challenges. The work on acid rain at Hubbard Brook demonstrates how long term research is used to identify a problem, propose a solution, track the success of that solution, and identify new issues to be addressed in further long term research¹³³. The acid rain research continues to resonate as a long-running example of how “cap and trade” approaches can be applied to many types of environmental pollution¹³⁴ and as an early example of the need to establish “critical loads” for air pollutants as a management tool¹³⁵. As noted above, understanding the importance of legacy phosphorus has contributed to assessment and management of lake eutrophication efforts across the world. Harvard Forest hurricane research – together with other LTER studies – has influenced policies regarding salvage harvesting and restoration following natural disturbance on public and private lands¹³⁶. Understanding of land use legacies has had important effects on forest management and conservation efforts across the U.S., from the forests of New England with long and complex human land use¹³⁷ to the old growth forests of the Pacific Northwest^{138,139}.

8 Biodiversity-Ecosystem Functioning Relationships

The relationship between biodiversity and ecosystem function ranks among the most important research issues in modern ecology because it brings together so many threads of ecological inquiry and, in an age of rapid biodiversity change and decline, has enormous ramifications for society. What are the patterns and controls on community diversity and how are they changing? Which key ecosystem services upon which society depends are regulated by biodiversity, and at what space and time scales? Do some species contribute disproportionately to ecosystem rates and transfers? Such understanding is key to predicting the functional consequences of changes in the distributions of species in response to environmental changes and management decisions, as well as to managing and restoring ecosystems to maximize food, fiber, and forage production and ensure the stability of crop yields in the face of environmental and economic perturbations.

Research on the relationship between biodiversity and ecosystem functioning has its roots in several intellectual and empirical movements. First, early ecologists struggled to understand the role of biodiversity in stabilizing populations and communities against perturbations¹⁴⁰⁻¹⁴². Second, agroecologists were interested in how practices such as intercropping, crop rotation, and other mixed cropping systems could alter total crop yields¹⁴³. Third, motivated by growing recognition that global environmental changes will have major effects on species interactions and distributions, ecologists recognized that species varied in ways that “mattered” for ecosystem processes and services (e.g., productivity, decomposition, and nutrient cycling) and called for increased biological complexity in models and for more research on the effects of community composition and species identity on ecosystem functioning¹⁴⁴.

LTER scientists have long played a central role in addressing these questions. One of the world’s first, most revealing, and most impactful large field biodiversity experiments was established at Cedar Creek in 1994, which demonstrated (and continue to show) a host of important consequences of higher species richness¹⁴⁵. Among them, more diverse plots were more productive and retentive of nutrients¹⁴⁶, had more stable productivity from year-to-year¹⁴⁷, and were more resistant to invasion¹⁴⁸. The experiment also inspired new theory that reconciled earlier work by May and McNaughton showing that diversity increased stability at the community level but decreased it at the population level^{149,150}.

Since then, LTER research has advanced and tested fundamental theory relating biodiversity and ecosystem functioning. We have been able to do this because effects of biodiversity on ecosystem stability can only be shown using long term datasets that include many years and encompass significant variation in the environment. In addition, different mechanisms play out over different timescales. For example, short term studies tend to be dominated by selection effects¹⁵¹ and show modest effects of biodiversity loss on productivity¹⁵². At Cedar Creek, two of the world’s longest running biodiversity studies showed that the effects of biodiversity on productivity strengthened over time, likely because of feedbacks related to soil fertility (Fig. 8-1)¹⁵³.

A similar pattern was observed over just three years in a crop diversity experiment at Kellogg Biological Station, supported by a growing mechanistic understanding of the factors controlling this relationship emerging in the next decade. Crop diversity was varied between one and six species by

adding rotations and cover crops and the highest corn yields were observed in the most diverse cropping treatment¹⁵⁴.

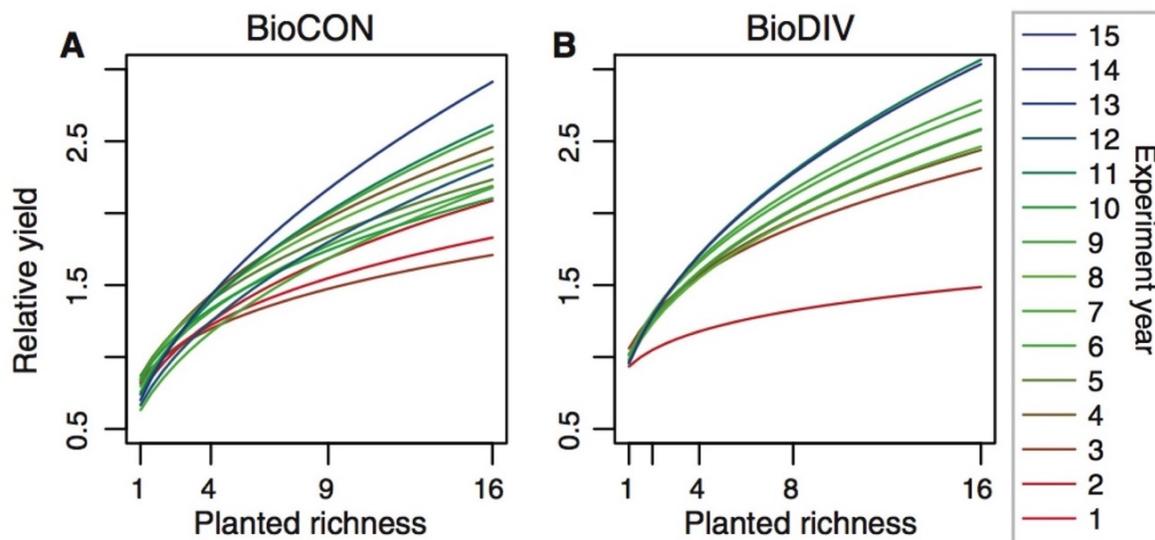


Figure 8.1. Steepening relationships between species richness and productivity (expressed as relative yield) in the original biodiversity experiment at Cedar Creek (BioDIV) (A) and the Biodiversity, CO₂, and Nitrogen (BioCON) experiment, also at Cedar Creek (B). From Reich et al. 2012.

In both the Cedar Creek biodiversity experiment and the Kellogg Biological Station crop diversity experiment, soils were strongly influenced by diversity treatments. At Cedar Creek, carbon sequestration rates accelerated over two decades, especially in species-rich plots where soil carbon accumulation rates were 200% greater in the second decade than the first¹⁵⁵. Greater plant diversity, through greater plant biomass, also led to greater fungal taxonomic richness¹⁵⁶. At Kellogg Biological Station, after 12 years, greater crop diversity increased soil carbon stocks, soil aggregation, and microbial activity, and altered microbial communities¹⁵⁷. LTER has also enabled comparison of biodiversity experiments with other long term studies that have shown that biodiversity in grasslands affected NPP as much as resources, disturbance, or herbivory¹⁵⁸ and that many species were necessary to maintain multiple functions across many years in ecosystems^{159,160}.

The biodiversity experiment at Cedar Creek inspired development of new analytical approaches for understanding mechanisms of biodiversity effects on ecosystem functioning¹⁶¹ and new experiments around the world such as BIODEPTH¹⁶² and Agrodiversity¹⁶³, networks of grassland experiments in Europe, the TreeDivNet network of forest biodiversity experiments^{164,165}, as well as experiments in marine¹⁶⁶ and freshwater¹⁶⁷ systems. LTER has been a key contributor to new studies exploring the importance of different aspects of biodiversity such as phylogenetic, functional, and, most recently, remotely sensed spectral diversity¹⁶⁸⁻¹⁷⁰, and revealed that these types of biodiversity sometimes showed stronger relationships with productivity than species richness.

Recent syntheses of biodiversity experiments demonstrated that in many cases, biodiversity increased not just mean productivity, but its stability, primarily by promoting resistance to climate events (wet or dry, moderate or extreme, brief or prolonged)¹⁸². The study also revealed that different environmental change drivers (e.g., nutrient enrichment, herbivory, elevated CO₂, disturbance) influenced ecosystem stability primarily through their effects on biodiversity – those that caused losses of diversity also destabilized the ecosystem most¹⁸³.

Findings from biodiversity experiments have begged the question of how important variation in biodiversity is in contributing to variation in productivity across landscapes outside of highly controlled experiments. This question inspired recent analyses of productivity data from regional to continental scale datasets, from the Nutrient Network, headquartered at Cedar Creek^{71,183,184} and from Global Forest Biodiversity Plots¹⁸⁵ that have shown positive diversity-productivity relationships that are consistent with experimental results.

LTER scientists have been leaders in applying biodiversity-ecosystem functioning research to inform societal needs, including detection of biodiversity across large scales, restoration of degraded habitats, and increased sustainability of fisheries and agroecosystems. For example, LTER has advanced new techniques for detecting biodiversity at scales relevant for addressing challenges facing society, using remote sensing^{186,187}.

LTER research is showing how greater diversity in agroecosystems can be used to increase the provision of ecosystem services, including crop yield, forage, and wood production; yield stability; pollination; and pest and weed suppression^{188,189}. For example, at Kellogg Biological Station, plantings of diverse prairie mixtures and switchgrass for biofuel feedstock, while they did not necessarily provide greater biomass, provided more methane consumption, pollination, grassland bird diversity, and pest suppression, than corn monocultures¹⁹⁰, and corn monocultures provided

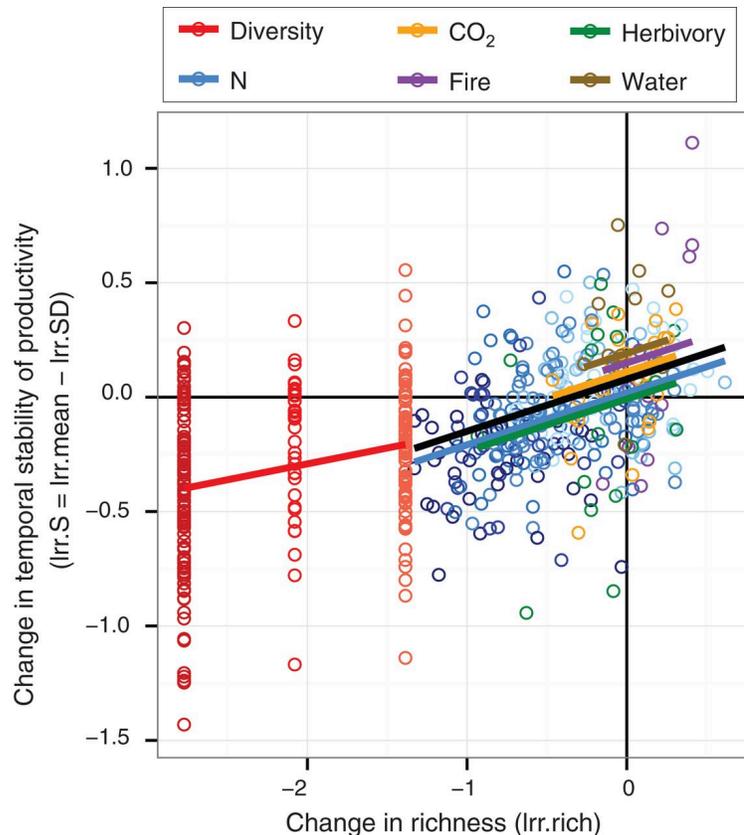


Figure 8.3. In a series of 12 decade-long experiments in temperate grassland, Hautier et al. (2015) manipulated nitrogen, water, carbon dioxide, herbivory, and fire. Effect of anthropogenic drivers of environmental change on the stability of productivity, as mediated by experimentally imposed changes in biodiversity [red line; slope and 95% confidence intervals (CIs): 0.14 (0.08 to 0.20)], or from biodiversity changes arising from anthropogenic drivers including N, CO₂, water, fire, and herbivory [black and other colored lines; slopes and 95% CIs: 0.22 (0.15 to 0.31)]. Black line is the fixed-effect linear regression slope across all anthropogenic drivers in the mixed-effects model; colored lines show trends for each driver. From Hautier et al. 2015.

more services when surrounded by landscapes with greater grassland cover. Recent studies are applying biodiversity and ecosystem functioning concepts in completely new fields and finding that diversifying fishing fleets can increase fishing yields and profits¹⁹¹ and that countries that produce a greater diversity of crops show greater year-to-year stability in total crop production¹⁹².

9 Physical, Chemical, and Biological Connectivity

While connectivity-oriented research within the LTER Network varies widely with respect to subject (i.e. demographic connectivity, landscape connectivity, hydrologic connectivity), these research efforts all provide rare, critically needed datasets for assessing climate change impacts on ecosystems properties and services. Connectivity among different components of landscapes (or seascapes) has long been recognized as a controlling factor with respect to species distributions, composition of biological communities, and structuring of ecosystems. As human activities continue to fragment all of earth's systems a mechanistic understanding of the function that connectivity plays in supporting key ecosystem processes and enabling adaptation to changing environments will be increasingly important. LTER research has already documented important climate-driven changes in connectivity that are helping scientists and society anticipate future challenges, but this will become an even more central role of LTER research as climate change accelerates.

The term connectivity varies somewhat in different fields, but in all cases, connectivity is scale and time dependent. For example, Leis¹⁹³ defined demographic connectivity as “the movement of individuals between populations in numbers large enough to be demographically significant”, Taylor¹⁹⁴ defined landscape connectivity as “the degree to which the landscape facilitates or impedes movement among resource patches”, and Pringle¹⁹⁵ defined hydrologic connectivity as “water-mediated transfer of matter, energy and/or organisms within or between elements of the hydrologic cycle”.

Short term studies have been able to address key aspects of scale-dependent connectivity, but longer term studies are essential to fully capture the temporal dynamics of connectivity. LTER programs are uniquely suited for studying these dynamics; e.g., variations in connectivity-altering events such as hurricanes and fires^{64,196}, modes of climate variability such as the El Niño¹⁹⁷, and directional shifts over longer timeframes linked to global change^{198,199}. The four examples described below, focusing on work conducted at SBC, JRN, ARC, and GCE, demonstrate how LTER programs are advancing our understanding of the roles that variations in connectivity play in shaping population, community, and ecosystem dynamics. In turn, this work informs ongoing conservation and natural resource management of some of the world's most important ecosystems: marine kelp forests, deserts scrublands, arctic streams, and coastal salt marshes and estuaries.

The Santa Barbara Coastal LTER program has conducted one of the longest and largest empirical tests of metapopulation theory to date^{200,201}. Santa Barbara Coastal researchers are examining how demographic connectivity among giant kelp (*Macrocystis pyrifera*) forests along a 500 km stretch of the California coast influences population dynamics. Analysis of a 22-year dataset showed that variations in connectivity among patches of giant kelp are strongly linked to rates of extinction and colonization (Fig. 1, left panel). Increasing levels of connectivity support higher probabilities of colonization and lower probabilities of extinction (Fig. 9-1 right panel). This study provided the first comprehensive evidence that kelp along the southern California coast function as one metapopulation system, challenging the view that local kelp populations are governed primarily by self-replacement. SBC developed an innovative measure of connectivity for this study that incorporates oceanographic transport and source fecundity. Variations in relationships between connectivity and population dynamics make it difficult to study metapopulation theory over short

time scales. Hence, the long term data collected by SBC are extremely valuable for making strong inferences about the role of connectivity in sustaining metapopulations. Such studies have been particularly scarce in marine systems.

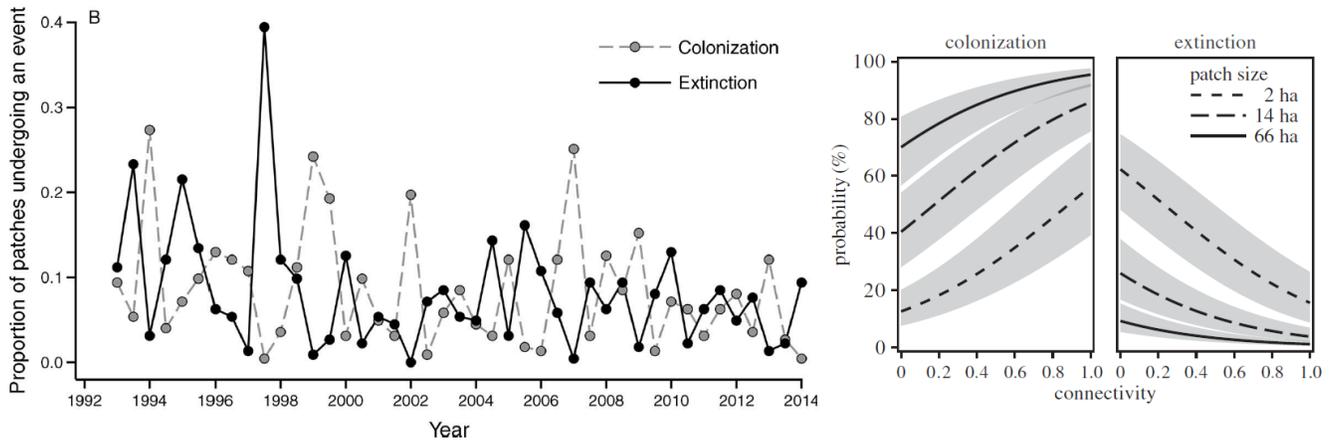
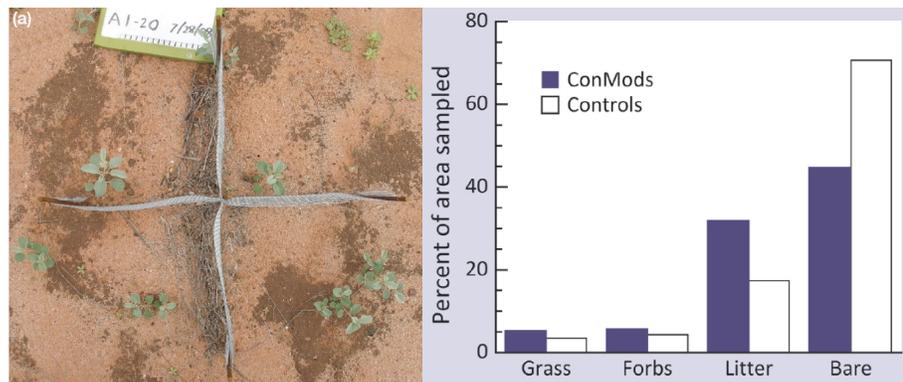


Figure 9.1. Left: Time series of the proportion of giant kelp patches that were colonized or went extinct during 6 month timeframes (from Castorani 2015). Right: Predicted probabilities of patch colonization and extinction as a function of patch size and demographic connectivity (from Castorani 2017).

Work conducted by the JRN LTER program has re-shaped our understanding of the role that connectivity plays in dryland environments. Early work on landscape connectivity in drylands, developed around the “fertile islands concept”, considered horizontal transport of materials at the plant-interspace scale^{202,203}. However, JRN investigators have demonstrated that simple scaling up of plant-interspace dynamics fails to explain broader patterns across the landscape. Hence, they have developed a new landscape connectivity framework for dryland ecosystems that links patterns and processes across multiple scales and explains the dynamics of these ecosystems more fully²⁰⁴. This framework considers soil, nutrient, and seed transport via wind and water flow, and incorporates both structural and functional (process-based) connectivity²⁰⁵. While the former refers to the extent to which spatial units are physically linked, the latter refers to how the connectivity occurs, for example addressing connections that arise during a particular transport event. This connectivity framework has been used to explain state changes within dryland ecosystems and to inform long term experimental work that is now underway at the

Figure 9.2. Left: Connectivity modifier (ConMod) at JRN showing foliar litter collection at base of mesh and germination of forbs within the affected area. Right: ConMods increase litter and decrease bare soil relative to control plots (from Okin et al. 2015).



JRN LTER site (Figure 9.2).

Many sites in the LTER Network are using river water chemistry as a tool for tracking watershed-scale changes in ecosystem structure, function and services. The ARC LTER, for example, is using long term data from rivers and streams in northern Alaska to track impacts of climate change on land-water connectivity. One of the longest records of river chemistry in the Alaskan Arctic comes from the upper Kugaruk River¹⁹⁸. Data from 1978-2014 collected by the ARC LTER program show increases in alkalinity, cation, and nitrate concentrations in the upper Kugaruk that are signals of permafrost thaw. Variations in constituent concentrations can be partly explained by variations in water discharge, but discharge-normalized concentrations in the upper Kugaruk have changed as well. For example, discharge-normalized nitrate concentrations have increased and discharge-normalized dissolved organic carbon (DOC) concentrations have decreased (Fig. 9-3). As permafrost thaws, water flow paths through soils deepen. This results in water that encounters different source materials and changes water travel times between soils and surface waters. Such changes in hydrologic connectivity have implications for productivity and food web dynamics¹⁹⁸ as well as microbial community composition²⁰⁶ (Crump et al. 2012). Crump et al.²⁰⁶ showed that patterns of microbial diversity in surface waters on Alaska's North Slope are structured by inoculation from microbial reservoirs in soils, followed by species sorting during down-slope dispersal through streams and lakes. Changes in water flow paths and travel times are therefore likely to be accompanied by changes in microbial community composition.

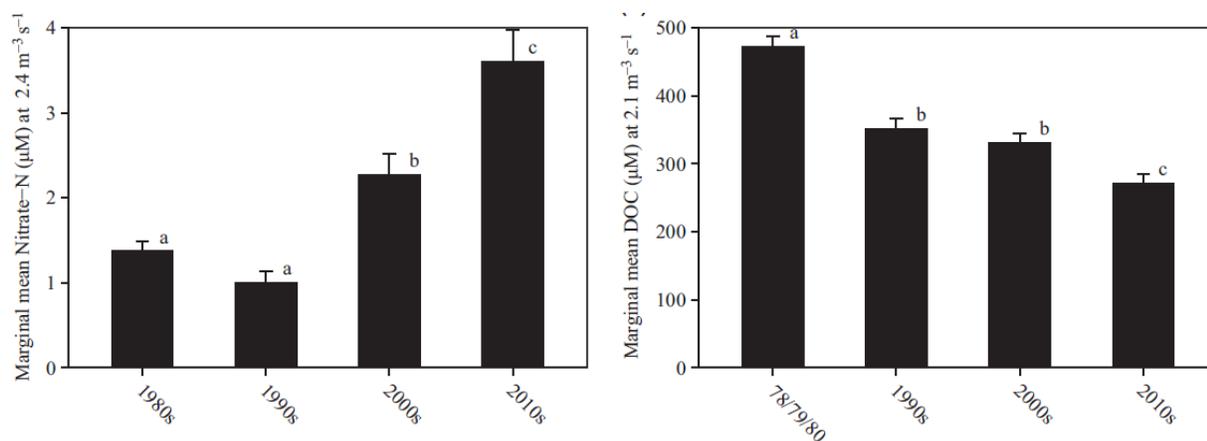


Figure 9.3. Long-term changes in discharge-normalized nitrate and DOC concentrations in the upper Kugaruk River (from Kendrick et al. 2018).

Understanding connectivity between watersheds and coastal waters, which is central to estuarine productivity, ecosystem dynamics and the coastal eutrophication problem²⁰⁷, is a core research objective shared by several LTER programs including BLE, FCE, GCE, and VCR. Recent findings from the GCE LTER program exemplify the value of long term studies focusing on land-sea connectivity. Data published in Wieski and Pennings²⁰⁸ show that annual net primary production (ANPP) of salt marsh grass (*Spartina alterniflora*) increases with increases in river discharge. Previous studies have identified sea-level anomalies as an important variable controlling marsh production^{209,210}. The GCE LTER study also found a relationship with sea level, but was novel in identifying river discharge as the most important driver of *S. alterniflora* ANPP. Long term data (2000-2011) were needed to capture a wide enough range of input variability to reveal the relationship. The importance of river discharge as a driver of *S. alterniflora* ANPP was corroborated using a remote sensing approach that extended the

analysis to 1984-2011¹⁹⁹. This longer study period also revealed a 33-39% decline overall in *S. alterniflora* ANPP over time, coinciding with an increase in drought frequency and intensity (Fig. 9-4).

The broader impacts of LTER-supported research on connectivity in ecological systems are far reaching and range from public education to guidance of policy and management decisions at local, state and national levels. They also include development of new conceptual models that are guiding research well beyond the LTER Network. For example, from the above case studies:

- New understanding of demographic connectivity among giant kelp forests from Santa Barbara Coastal LTER research is informing design and assessment of Marine Protected Areas along the California coast. Santa Barbara Coastal's work has also provided a rare example and model for field studies of meta-population theory that is guiding new research on demographic connectivity in other ecosystem types.
- Jornada LTER's research on landscape connectivity is informing landscape management decisions, both in terms of optimizing agricultural production and suitability of arid lands for restoration in the southwestern United States. Their work to develop a new conceptual framework that addresses patterns and processes of connectivity across multiple scales is also informing international efforts to address challenges associated with expanding desertification globally.
- The Arctic LTER has served as a rare test bed for hypotheses about climate change impacts on hydrologic connectivity in permafrost landscapes, and their research has greatly facilitated the development of tools and approaches for using water chemistry to track catchment-scale changes in the Arctic.
- Georgia Coastal Ecosystem LTER's research on land-ocean connectivity is informing science-based management of coastal resources in Georgia and the southeast region more generally. This is, in part, accomplished through Georgia Coastal's participation in and partial funding of the Georgia Coastal Research Council (www.gcrc.uga.edu/). This council, which currently has 168 affiliate scientists and coastal managers, hosts workshops, assists management agencies with scientific assessments, and synthesizes coastal research.

LTER-driven refinement of conceptual models related to different types of connectivity has set the stage for major advances in system-level understanding that incorporate linkages between demographic, landscape, and hydrologic connectivity. These have largely been studied as separate subjects in the past, but the LTER Network is well positioned to lead synthesis efforts that integrate across these research areas as we move forward. Looking ahead, we anticipate continued rapid advances in LTER connectivity research thanks to improvements in technologies that support population connectivity studies (e.g., genomic analysis, lightweight GPS tracking devices), hydrologic studies (streaming sensor technologies and autonomous submersibles), and landscape connectivity (facilitated by new remote sensing technologies).

10 Coupled Social-Ecological Systems

As humans have increasingly come to dominate global ecosystems, there is a new urgency to understanding and managing feedbacks between humans and the ecosystem services on which we depend. Only through such understanding can society make choices that confer sustainable benefits to both people and ecosystems. To this end, long term interdisciplinary research is essential to understand both human influences on the environment and the resultant feedbacks between environmental change and human behaviors, decision making, and well-being ²¹¹.

Sustainability science developed rapidly during the 1990's and early 2000's to advance understanding of the complex interactions between humans and ecosystems and to help address urgent environmental challenges²¹². During that time ecologists and social scientists collaborated to articulate an interdisciplinary research agenda for integrated social-ecological research that emphasized multiple scales of human-environment interactions, feedbacks between the environment and human behavior and decision making, and system inertias and lags in those feedbacks^{4,213}.

Research into coupled social-ecological systems requires a re-framing of the way ecologists view human-ecosystem interactions from humans as exogenous drivers of ecosystem change to humans as interactive components of ecosystems^{214,215}. Many LTER researchers and sites have been deeply involved in accelerating this paradigm shift²¹⁶. Since 1997, the urban LTERs in Baltimore and Phoenix have been funded to conduct both ecological and social-ecological research. The Kellogg Biological Station site takes a social-ecological approach to study the delivery of ecosystem services by agricultural landscapes²¹⁷. Beginning in 1996, two sites (Coweeta and North Temperate Lakes) received annually augmented funding to pursue regionalization and social science research. In 2006, the Florida Coastal Everglades site (FCE) expanded to include social-ecological research; the title of their recently published synthesis book is "The Coastal Everglades: The Dynamics of Social-ecological Transformation in the South Florida Landscape"²¹⁸. Other LTER sites have leveraged non-LTER funding to also undertake social-ecological research: For example, seven sites (Harvard Forest, H.J. Andrews, North Temperate Lakes, Central Arizona-Phoenix, Bonanza Creek, Coweeta and Hubbard Brook LTERs) have developed social-ecological scenarios of long term ecosystem dynamics²¹⁹ and five sites (Baltimore, Phoenix, Cedar Creek, Florida Coastal Everglades and Plum Island Ecosystem) are involved in Macrosystems Biology research on the social-ecological dynamics of American residential landscapes²²⁰.

Over the past decade, contributions from LTER social-ecological research have included the development of new conceptual frameworks and modeling approaches, many site-specific discoveries, influential cross-site syntheses, and accompanying societal impacts. Examples of conceptual advances include:

- A conceptual framework for long term social-ecological research that integrates the biophysical and social sciences through an understanding of how human behaviors affect “press” and “pulse” dynamics, ecosystem processes, and ecosystem services with feedbacks to human behaviors and well-being⁴.

- A social-ecological model of residential landscapes that relates household-scale decisions regarding outdoor space to multiple scales of social drivers ranging from distinct landscape patches within parcels (e.g. front versus backyards), to households, neighborhoods, and regions²²¹ (Figure 10.1).
- A framework that articulates the transformational nexus of urban ecology and design to advance contemporary resilience and future sustainability of cities^{222,223}.
- A social-ecological approach to row-crop agriculture that simultaneously considers natural and human factors across a mosaic of agricultural and non-agricultural land covers, elucidating social-ecological mechanisms that contribute to the resilience of important populations and processes in agricultural landscapes^{217,224}.
- A new synthesis of urban ecology toward a science of cities that brings forward the built aspect of these systems, identifying cities as social-ecological-technological systems (SETS)²²⁵.
- Articulation of a new urban systems science to understand the emergence of novel ecosystems in relation to human values and perceptions²¹⁵.
- A conceptual model of “dynamic heterogeneity” of urban ecosystems as the interaction of material flows, species community assembly processes, and spatial land use choices²²⁶.
- Exploration of the applicability of the ecological concept of disturbance to urban social-ecological systems²²⁷.
- A framework that articulates the transformational nexus of urban ecology and design to advance contemporary resilience and future sustainability of cities^{222,223}.

The urban LTER sites have yielded important insights into human-environment interactions across a range of settings. The Baltimore Household Telephone Survey and the Phoenix Area Social Survey have provided novel information on environmental knowledge, perceptions, values, and behaviors; how these influence ecosystem structure and function; and how changes in ecosystem structure and function may affect physical activity, social cohesion, perception of neighborhood desirability, and willingness to relocate²²⁸. In Phoenix, Ripplinger et al.^{229,230} used long term vegetation data to examine plant diversity trends and responses to a sudden economic disturbance – the 2008 Great Recession – in the Phoenix social-ecological system. They found that massive foreclosures and home abandonment led to widespread loss of yard management (irrigation, weeding, planting, fertilizing) that drove an increase in post-recession plant species richness and community homogeneity as abandoned yards were taken over by annual, weedy species. In all of these examples, the urban LTER sites have established long term data streams that provide novel insights into how urban ecosystems are changing in response to complex social-ecological drivers and that raise new questions that can only be addressed with continued long term research.

Work at the urban LTERs has also elucidated social-ecological mechanisms driving changes in urban biodiversity. For example, in a CAP experiment manipulating food resources and predation, Bang et al.²³¹ showed that bottom-up factors strongly regulated plant-associated arthropod communities in desert habitats while urban arthropods responded to a complex set of relationships among climate, human-managed plant growth, and predation. Also at Phoenix, long term monitoring of 12 riparian sites along a hydrologic and urbanization gradient has shown that designed and managed sites supported more broadly distributed generalists while unmanaged native desert sites supported more

specialists²³². Simultaneously, the urban, unmanaged wetland sites provide refuge for people experiencing homelessness²³³.

Research on the American residential macrosystem has characterized a continental-scale ecological homogenization where residential ecosystems in diverse hydro-climatic regions are more similar to each other than the native ecosystems that they replaced. This has implications for plant

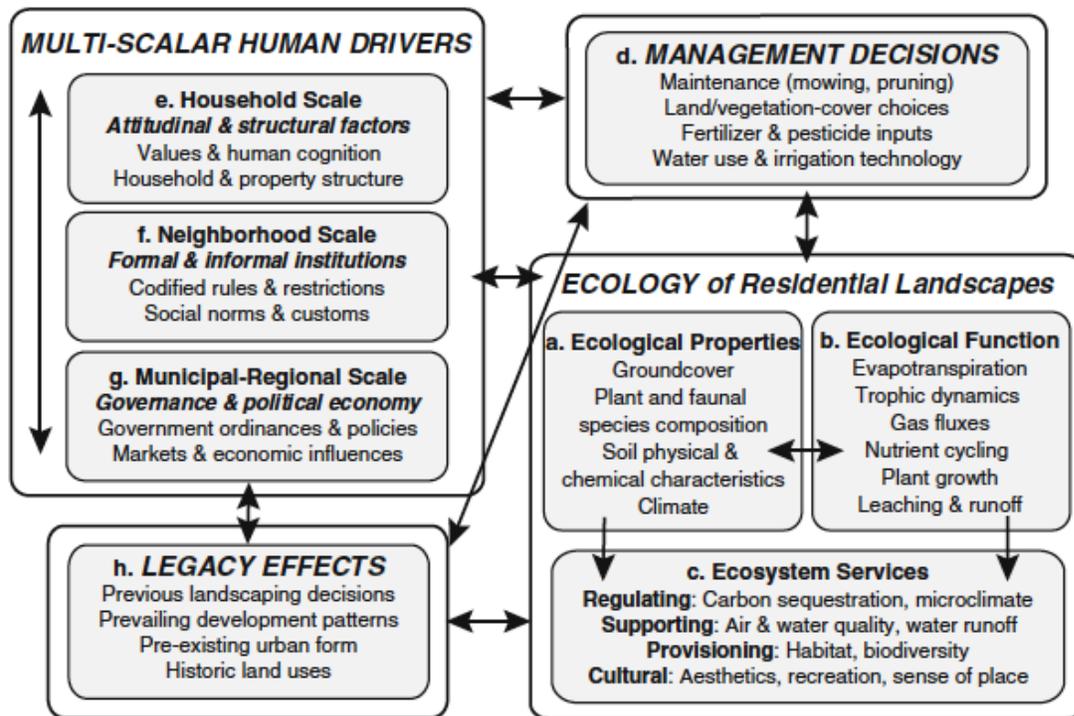


Figure 10.1. From Cook et al. (2012). Conceptual framework of multi-scalar and social-ecological interactions of residential landscapes. Arrows represent interactions between framework components.

biodiversity, soil carbon and nitrogen dynamics, microclimate, hydrography, and human satisfaction and well-being²²⁰.

LTER research has shed important light on the coupling between environmental change, market forces, and human decision-making regarding land management. For instance, researchers at Harvard Forest incorporated results from forest landowner surveys into landscape models to reveal important feedbacks between tree mortality caused by forest invasive pests and tree harvest patterns and rates, with local- and regional-scale impacts on forest conditions and ecosystem services²³⁴ (Figure 10.2). At Kellogg Biological Station LTER, research has revealed social and environmental factors affecting farmer willingness-to-participate in payment-for-environmental-services programs such as the Environmental Quality Incentives Program (EQIP). They found that willingness-to-participate was best approached and modeled as a 2-stage process that first identified farmers who were at least willing to consider participation, and then considered factors that could deter those individuals from participating (e.g., farm size, proportion of farm under irrigation, and

farm income²³⁵). These are inherently long term questions and the LTER Network is providing a novel and important platform for addressing issues central to sustainability science.

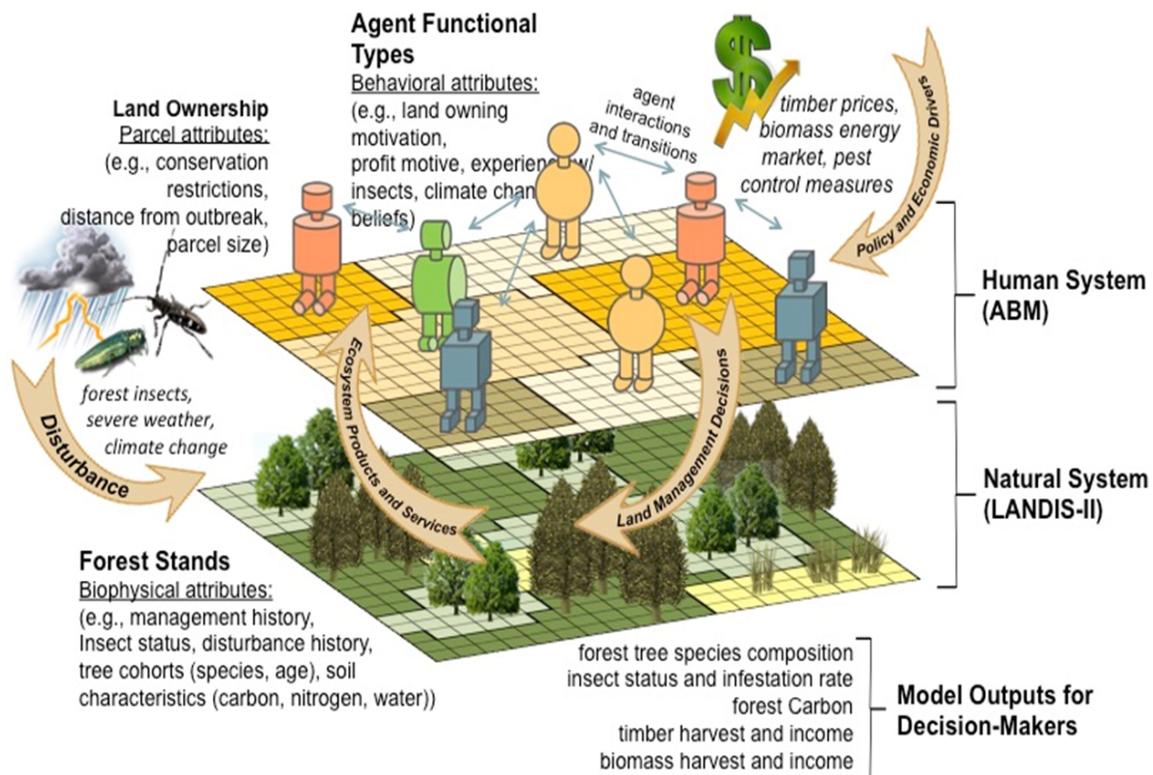


Figure 10.2. Conceptual model of the dynamic relationships between landowners, forest pest and pathogens, and the structure and composition of New England forests. The research by Holt et al. (2019) has helped elucidate the drivers and consequences of tree harvesting by exploring decision-making among different types of landowners in response to a variety of exogenous and endogenous forces. The studies are actively developed with public and private resource managers, extension service professionals, and landowners so that the results address real problems and are received by an engaged audience.

Many of the activities described above involved extensive, meaningful engagement with regional stakeholders such as educators, landowners, industrial representatives and government agencies. LTER social-ecological research has often been highly translational²³⁶ and offered numerous entry points for LTER science to inform regional policy and management. For example, LTER scenarios have all been co-produced with diverse stakeholders, providing an avenue to bring socio-ecological perspectives to longstanding regional issues and concerns²³⁷. At KBS, researchers have partnered with agricultural professionals and industry to develop a carbon credit protocol for agricultural nitrogen management, and have conducted surveys and discussion forums for scientists, farmers, extension educators, government and state agency staff, industry, and private-sector farm advisors. The Science and Policy Exchange (<https://science-policy-exchange.org>) was created as a platform for northeast LTERs to share research on forest management, pests and pathogens, alternative landscape futures, and many other societal issues.

Looking forward, it is clear that ecosystem dynamics at LTER sites are increasingly being conceptualized as manifestations of coupled social-ecological systems. Scale-dependent lags and inertias in both social and ecological responses make the study of coupled social-ecological systems a particularly daunting scientific challenge. At the same time, these broadly interdisciplinary approaches to long term research are critical for enhancing the social relevance of scientific findings. Because of the long term nature of LTER research, as well as deep site-based knowledge that helps to identify appropriate spatial and -temporal scales of analysis, the LTER Network is well poised to continue to advance social-ecological systems theory and its application to the design and management of sustainable environmental futures.

11 Resistance, Resilience & State Change

Understanding resistance and resilience – the abilities of ecosystems to withstand or recover from disturbance – is an enduring basic science challenge in ecology, with great practical importance at a time when critical natural and cultural landscapes are experiencing extremely rapid and large environmental changes, stresses, and disturbances. Multi-decadal LTER studies have provided important insights into mechanisms that confer resistance or resilience to physical and biological perturbations across diverse ecosystems. This research has informed policy and management including developing formal methods for characterizing ecological transitions²³⁸, guiding design of early warning systems to anticipate ecosystem state changes²³⁹, identifying anticipatory management strategies to prevent undesirable ecosystem state changes^{240,241}, and guiding restoration to more desired ecosystem states²⁴².

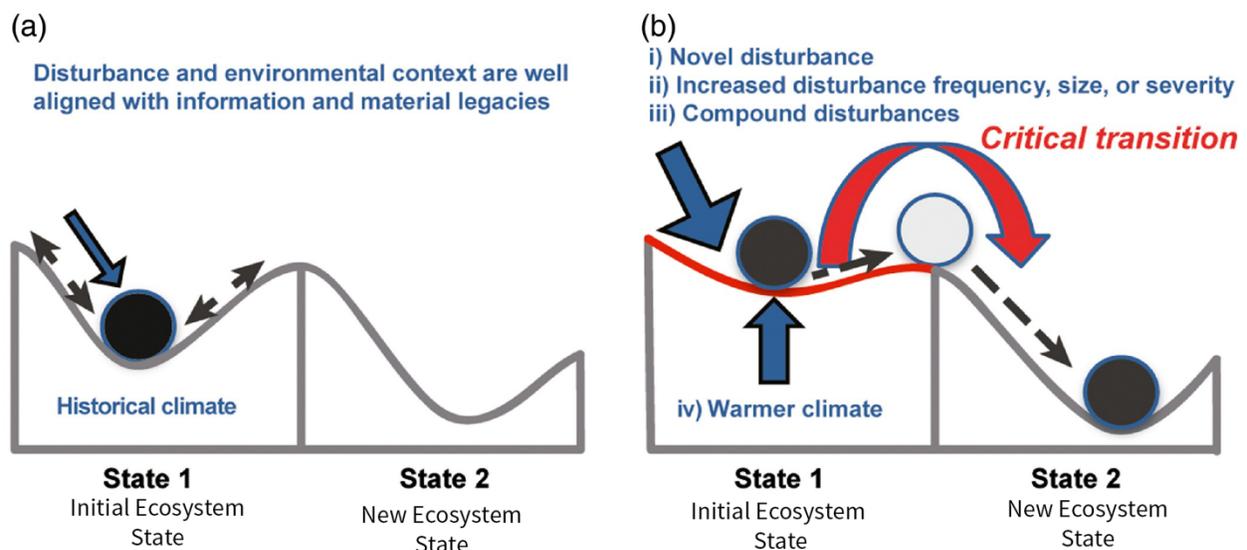


Figure 11-1. Conceptual representation of ecosystems (black ball) within a theoretical landscape of alternative ecosystem states (valleys separated by peaks). (a) Ecosystems are resilient to disturbances lying within the safe operating space, indicated by disturbances that may move the system but not cause it to shift to another state. (b) Ecosystems are likely to shift to a different state in response to four hypothesized mechanisms (i–iv) that move a system outside its safe operating space and trigger a shift to a different state. Adapted from Johnstone et al 2016.

A resilient ecosystem returns to its original structure, function, and services, perhaps after time lags, based on the severity of the disturbance. An ecosystem that does not maintain or revert back to its original state after the disturbance experiences a regime shift, existing in a new state which may or may not be stable¹¹⁷ (Figure 11-1). Short-lived disturbance events (e.g., hurricane, fire, ice storm) are referred to as “pulse” events and on-going disturbances (e.g., pest infestations, climate change) are “presses.” Both types can generate enduring legacies that shape ecosystems for decades or much longer (see Section 7). Trajectories of ecosystem change depend on initial ecosystem properties and the types of disturbance that the ecosystem experiences^{117,118}. When industries and livelihoods depend on the initial ecosystem state, abrupt ecological changes can have especially profound societal implications – such as loss of enjoyment and revenue from tourism, subsistence harvesting,

fisheries, and timber harvest. Here we illustrate these concepts and LTER's contributions to resilience research and its application for two coastal sites (Virginia Coastal Reserve and Moorea Coral Reef), a tropical forest ecosystem (Luquillo Experimental Forest) and the McMurdo Dry Valleys in Antarctica.

At the Virginia Coast Reserve, a long-term landscape-scale experiment has documented the impact of marine heatwaves on seagrasses in the shallow lagoons landward of the barrier islands. Seagrass in the Virginia Coast Reserve lagoons became locally extinct in the early 1900s as a result of disease and hurricane disturbance. The lagoons remained in this non-vegetated state for several decades due to seed limitation – until a landscape-scale experiment restored nearly 25 km² of seagrass habitat by seeding²⁴³. Development to a mature seagrass-vegetated state took approximately one decade²⁴²; five years later a marine heatwave decimated seagrass populations in some areas (Figure

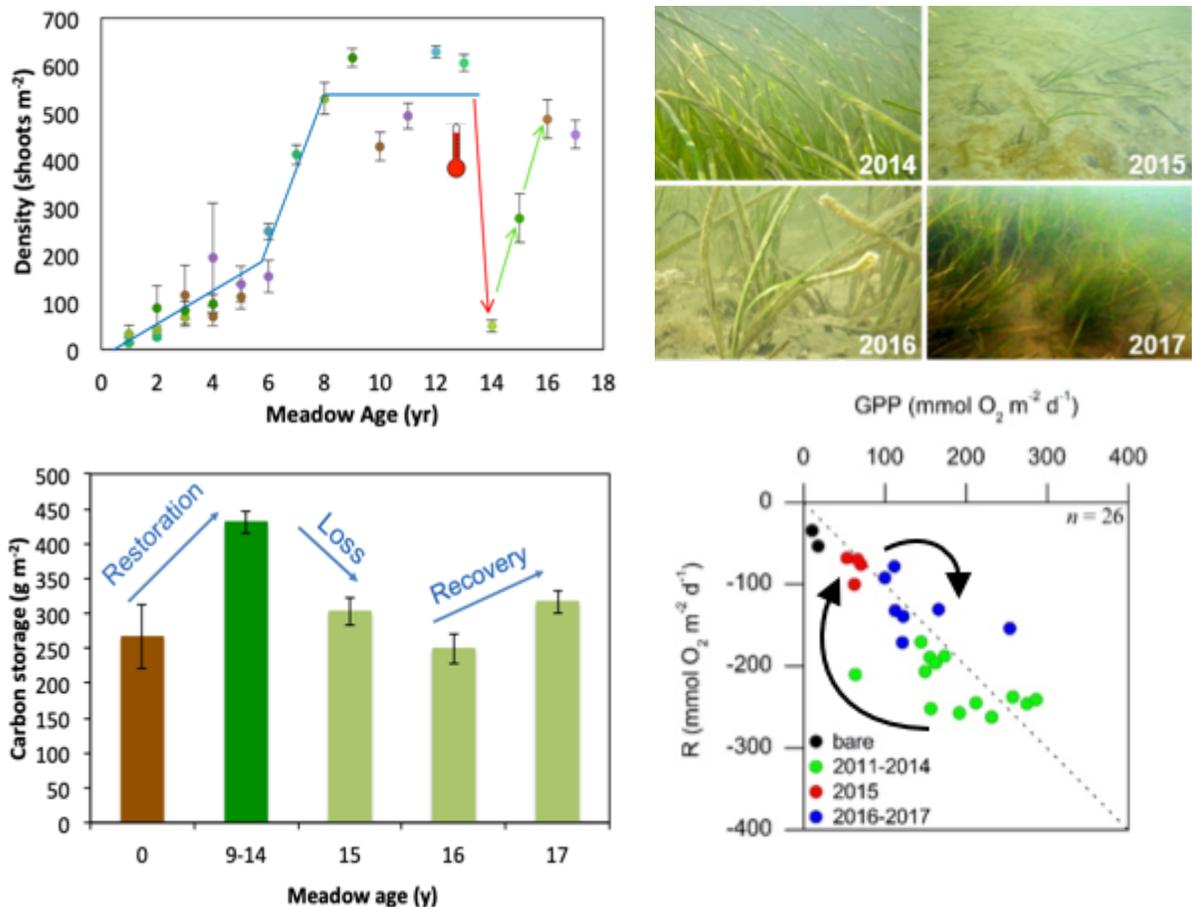


Figure 11-2. Seagrass die-off and recovery at the Virginia Coast Reserve (VCR) LTER site. Long term monitoring of sea grass density revealed a negative response to a single year of elevated coastal water temperatures. Images from 2014-2017 (upper right) show the loss and recovery of the seagrasses. Carbon storage (i.e., photosynthesis, lower left) directly responds to seagrass biomass (shoot density, upper left). Furthermore, rates of seagrass metabolism (gross primary productivity and ecosystem respiration, lower right) were restored after recovery from disturbance. Thus, resilience of ecosystem population (seagrass) and functions (carbon storage, metabolism) was fairly rapid in response to the disturbance of a single year of elevated sea temperatures.

11-2). Plant density dropped to less than 10% of steady-state levels prior to the heatwave, and in just one year, nearly all of the carbon accumulated in the meadow sediments over 15 years was lost.

The sudden die-off of seagrass at Virginia Coast Reserve provided a unique opportunity to study resilience to marine heatwaves. Seagrass density recovered to 80% of pre-disturbance levels in only two years. Sediment carbon storage lagged plant recovery, as sufficient seagrass canopy cover is needed to slow currents and enhance organic matter accumulation and burial over time. Carbon sequestration in plant biomass measured using a novel underwater eddy covariance system^{244,245} was reduced by 60% in the die-off year and recovered to within the range of mature meadows two years later. Spatial variance in heat wave intensity and in seagrass recovery illustrated resilience at the landscape scale²⁴⁶. The identification at the Virginia Coast Reserve of tipping points in water temperature, water clarity and depth beyond which seagrass cannot recover from disturbances has informed seagrass restoration and coastal resilience planning in similar environments in both the eastern U.S. and abroad.

The Moorea Coral Reef LTER has shifted scientific paradigms regarding how coral ecosystems respond to extreme disturbances such as hurricanes, and to chronic stressors such as eutrophication, fishing, ocean acidification, and rising ocean temperature. The speciose coral communities of the offshore reefs (forereefs) of Moorea have generally proven resilient to massive disturbances. The last decade provided a severe test of this resilience, as a coral-eating seastar outbreak and cyclone virtually eliminated corals from the forereefs⁸⁸. Surprisingly, ensuing recovery of corals was more rapid than has been documented anywhere in the world^{88,247} (Figure 11-3). This

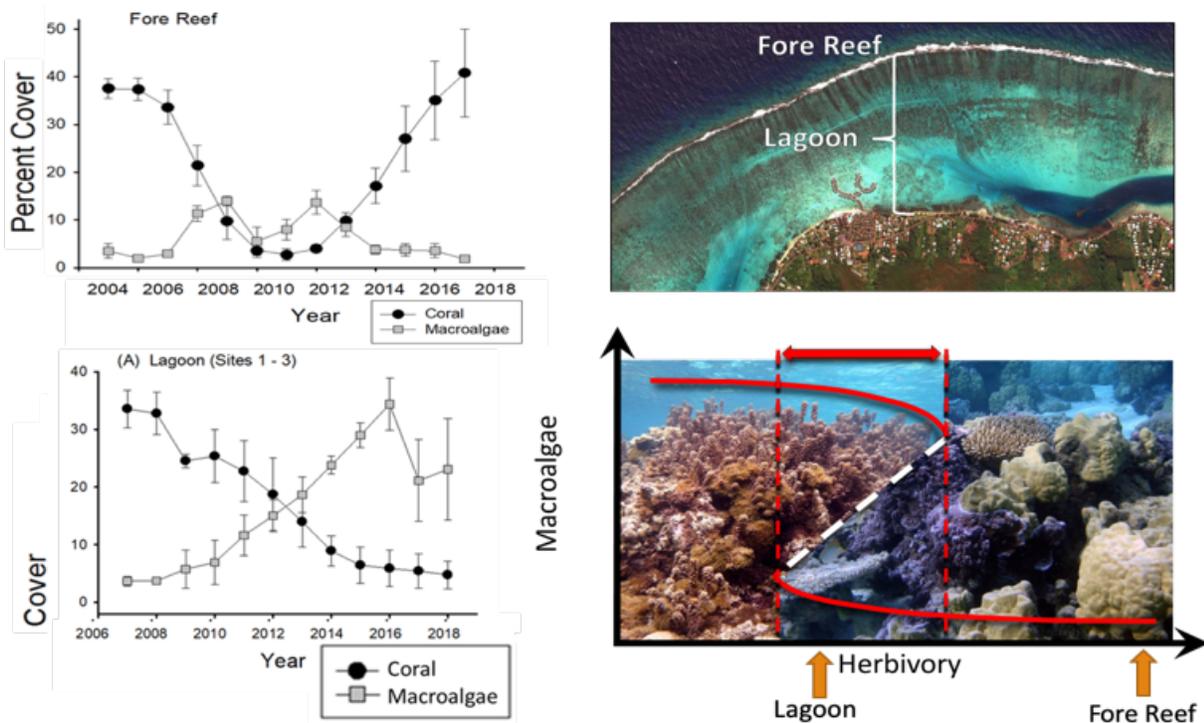


Figure 11-3. Changes in percent cover of coral and macroalgae in the forereef and lagoon. Coral coverage responded quickly after reaching a low in 2011 in the forereef, whereas in the lagoon there has been a continued decrease in coral coverage with increasing macroalgae. Adapted from Schmitt et al. 2019.

resilience was conferred by an increase in herbivorous fishes that kept reefs in an algal-free state, thereby allowing rapid coral recruitment and the full recovery of coral cover^{88,248}. In contrast, the heavily-fished nearshore lagoonal reefs at MCR that were depleted of herbivorous fish also suffered near-elimination of corals but shifted from a coral-dominated to a stable algal-dominated ecosystem²⁴⁰. This phase shift was well-documented by long term observational data, and the underlying mechanism (herbivory) was clearly demonstrated by field experiments. The findings from this research have broad management ramifications given the increasing occurrence of shifts from coral- to algal-dominated reefs in tropical systems worldwide. As Schmitt et al.²⁴⁰ point out, knowing the underlying mechanism provides an opportunity for “anticipatory management” to reduce the odds of such undesirable state shifts.

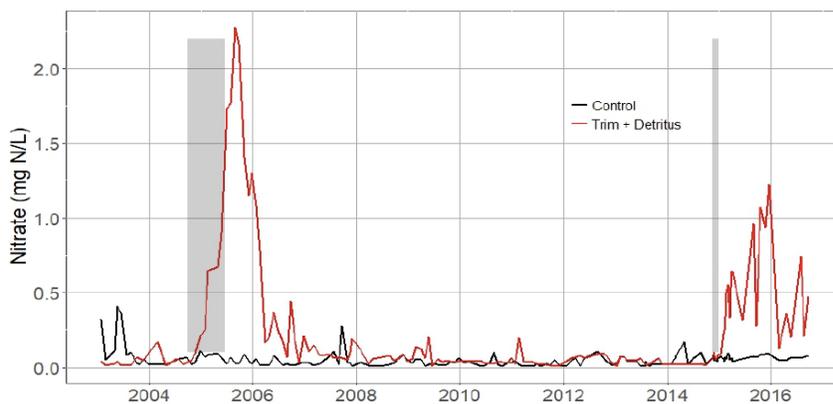
Hurricanes affect nearly every continent in the world and are among the most intense weather disturbances in forest ecosystems^{249,250}. Global climate models generally project an increase in the frequency of severe storms in the Caribbean and other regions^{251,252}, so understanding forest resilience and recovery mechanisms to severe storms is especially timely.

The Luquillo LTER program has developed a relatively long record of the ecological effects and recovery processes from hurricanes in a tropical forest ecosystem. Investigations into impacts of Hurricanes Hugo and Georges quantified the effects of increasing hurricane frequency and intensity^{253,254}. Historically, forest processes such as soil nutrient cycling and stream chemistry export returned to near pre-hurricane levels quickly (months), exhibiting a high degree of resilience²⁵⁵⁻²⁵⁷. Other factors, such as forest structure, stream-water exports of coarse particulate matter, and abundances of some plants and animals, recovered slowly or never fully recovered their pre-hurricane conditions^{258,259}. Forest canopy opening and detrital inputs were the dominant drivers of ecosystem response to disturbance^{256,260-263}.

Early results at Luquillo prompted the development of long term manipulative experiments (Canopy Trimming Experiments) to explore the separate and combined effects of canopy opening and detrital deposition. In general, canopy openness has proven a more important predictor of ecological response, favoring pioneer trees, reducing the abundance and diversity of key animal groups, reducing decomposition rates via inhibition of lignin-degrading fungi, and increasing nitrate export in soil water²⁶⁴. Researchers also detected a large flush of labile carbon and nutrients leached into soil from the deposited litter within three weeks following the experimental trimming of the canopy. Soil microbial biomass increased quickly. Soil water closely mimicked the response of stream chemistry to hurricane disturbances²⁵⁷. These results demonstrated the strong hurricane-mediated connection between forest and stream biogeochemistry in this rainforest system. More generally, decades of observational and experimental research at Luquillo have demonstrated the remarkable resistance and resilience of wet tropical forest ecosystems to environmental change²⁶⁵. Ongoing experiments manipulating temperature and precipitation are testing the vulnerability of this ecosystem to changing climate and disturbances to inform the development of adaptive forest management strategies²⁶⁵.



Figure 11-4. Hurricane disturbance in the Luquillo Experimental Forest following the passage of Hurricane Maria. (Left) A forest scene one week post-hurricane, showing the open canopy and hurricane debris typical of most areas (J. Zimmerman photo). (Right) A debris dam on the Prieta Stream with a 1 x 1 meter quadrat for scale (Pablo Gutiérrez photo). Changes in mean concentrations of nitrate in three replicate blocks of the Canopy Trimming Experiment, contrasting control (green line) and trimmed (red line) plots where the canopy was trimmed by arborists and the detritus was placed on the ground to simulate hurricane conditions. Gray bars indicate treatment periods in 2004-5 and 2014.



At the extreme opposite end of the spectrum of global ecosystems, LTER science at McMurdo Dry Valleys (MCM) is discovering how polar desert ecosystems are responding to changing climate and climatic perturbations. In this cold (-18°C mean annual air temperature) and dry ($<5\text{cm}$ snow water equivalent/year) environment, soils are inhabited by a few taxa of nematodes, rotifers, and tardigrades, and glacial meltwater streams host thick benthic cyanobacterial mats. During a decadal cooling trend, populations of soil taxa and biomass of stream benthic algae decreased²⁶⁶. This climatic disturbance abruptly ended in January 2002 when a short period of very high glacier melt generated record-high streamflows and increased soil moisture across this landscape. Compared to the decade prior to flood year, the decade following this extraordinary season had stable mean summer air temperatures and increased mean solar radiation flux²⁶⁷ – both of which are important contributors to glacial surface melt. Stream algal mat biomass began to recover in the several years after 2002, and *Scottnema* sp nematode populations reach a minimum during 2002. The resilience of these polar desert stream and soil ecosystems was somewhat slow, compared to the other examples presented in this section. Ultimately, we expect this is due to the fact that stream benthic mats grow slowly²⁶⁸, and that soil nematodes have a life span of approximately 7 years. These results demonstrate surprising ecosystem resistance to large perturbations in such a harsh environment.

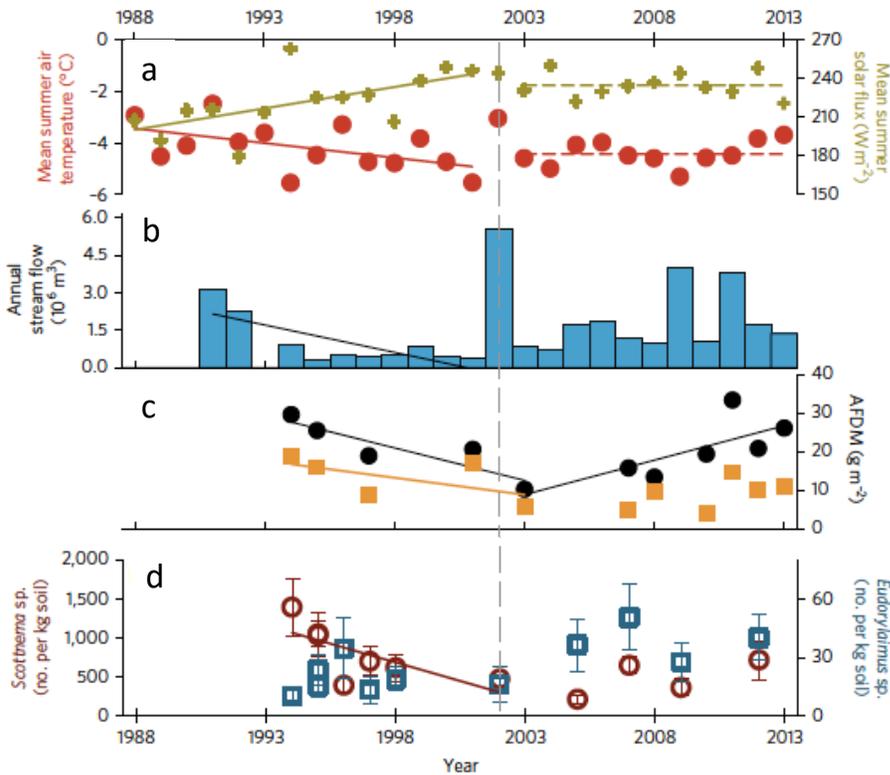


Figure 11-5. Soils and streams in the McMurdo Dry Valleys (MCM) Antarctica react to a summer air temperature cooling trend prior to 2002, a) austral summer air temperature and solar radiation means, b) total streamflow generated annually for streams of a single lake basin, c) stream benthic biomass (ash-free dry mass of Phormidium-dominated mats in orange and Nostoc-dominated mats in black), and d) populations of Scottinema sp (circles) and Eudorylaimus sp (squares).

Overall, long term monitoring has allowed LTER researchers to characterize a variety of ecosystems both before and after disturbance, capturing valuable information about responses to gradually varying conditions and extreme events. Using long term manipulative experiments together with observations, LTER investigators are able to deliberately alter factors such as initial conditions, severity and frequency of disturbance, and potential stabilizing forces (e.g. diversity, resource stocks, etc.) to identify signs of impending transition, thresholds beyond which ecosystem transitions may be likely.

12 Evolution in Long Term Ecological Experiments

Understanding the resistance and resilience of foundation species such as dominant plants and corals to climate change is a critical scientific and societal issue because the loss of these species could fundamentally reshape communities and ecosystem processes. One of the most exciting advances in the LTER Network over the past 10 years has been the growing involvement of scientists from diverse areas of ecology, including population, community and evolutionary ecology. This convergence of scientific perspectives has stimulated LTER research on rapid ecological evolution, and is beginning to yield important insights into adaptive capacity of species under rapid environmental change and its implications for ecosystem functions and services.

While much LTER research has focused on community and ecosystem ecology, LTER sites are also excellent laboratories for studying evolution in the wild. Because treatments have been imposed on replicate plots (populations) for decades, researchers can sample populations from different treatments and test for genetically-based differences in phenotypic traits and/or can use genomic approaches to test for genetic differences among populations. Repeated calls have emphasized the need to identify the environmental factors driving natural selection in nature^{269,270}, and long-running manipulative experiments like those at many LTER sites can help reach that goal. New work is capitalizing on LTER site experiments to test theoretical predictions about the evolution of cooperation, to consider how community context (presence and abundance of interacting species) influences adaptation to the abiotic environment, and to investigate the demographic and ecosystem consequences of adaptation.

In 1988, Richard Lenski began his famous *E. coli* long term evolution experiment. This experiment showed that by continuously evolving replicate populations, we could make fundamental advances in our understanding of evolution, such as how a single mutation can totally shift a species' niche²⁷¹ or how adaptation appears to be limitless with populations continuously increasing in fitness even after thousands of generations²⁷². These same approaches are inadvertently applied throughout the LTER Network. Because the LTER was not originally designed for studying evolution, sample populations were not initially archived; however, evolutionary changes can still be quantified by comparing control populations to treatment populations. In collaboration with museum facilities with divisions of genomic resources, some sites (e.g., Sevilleta LTER) have begun to archive tissues and DNA and create phenotype databases for long term evolutionary monitoring, and others are storing seeds and tree cores in anticipation of future resurrection experiments (Kellogg Biological Station and Hubbard Brook LTERs). Several other studies have applied approaches from quantitative and molecular genetics to tap the potential usefulness of LTER experiments for the study of evolution. We provide several examples below.

High levels of population genetic diversity may buffer foundation species against climate disruptions, but strong directional selection associated with climatic extremes may also rapidly reduce such diversity. For example, the foundation plant black grama grass (*Bouteloua eriopoda*) dominates southwestern North American grasslands. Genotyping-by-sequencing demonstrated unexpectedly high genetic variability among black grama plants in a 1 ha site within the Sevilleta National Wildlife Refuge in central New Mexico. Three years of an extreme growing season drought experiment reduced black grama survival and biomass, with clear genetic differentiation (higher F_{ST}) between

plants succumbing to drought and those remaining alive. Reduced genetic variability in the surviving plants in drought plots indicated that the experimental drought had forced black grama populations through selection bottlenecks²⁷³. Similarly, genetic variation has been detected in coral responses to temperature, which may allow for rapid adaptation to global warming²⁷⁴. Such rapid adaptation has the potential to increase resilience, providing a mechanism of recovery after extreme diebacks. For example, grazing pressure and cyclones caused dramatic declines in coral cover (nearly 50% cover to <3% cover over 5 years), but populations rebounded in the following years. Population densities showed the U-shaped pattern of abundance over time that is characteristic of populations experiencing evolutionary rescue (Figure 12.1), although further data on shifting genotype frequencies is needed to definitively attribute the recovery to evolution rather than demographic rescue²⁴⁷. Interestingly, because strong selection erodes genetic diversity, these evolutionary responses to strong disturbances may limit evolutionary responses to other environmental changes. Because many LTER sites include experiments factorially simulating environmental changes, they are uniquely suited for addressing this question.

Plant-rhizobia and plant-mycorrhizae interactions are classic examples of mutualisms, where plants trade carbon fixed through photosynthesis for nitrogen and/or phosphorus acquired by rhizobia and mycorrhizae. Theory on the evolution of resource mutualism predicts that nutrient addition will destabilize resource mutualism and select for less cooperative rhizobium or mycorrhizal partners. Rhizobium populations isolated from a long term N-addition experiment at Kellogg Biological Station LTER provided the first empirical test of these predictions and showed that rhizobia from N-addition plots provide substantially fewer growth benefits to plant hosts²⁷⁵ (Figure 12.2). Additional work has identified the genes

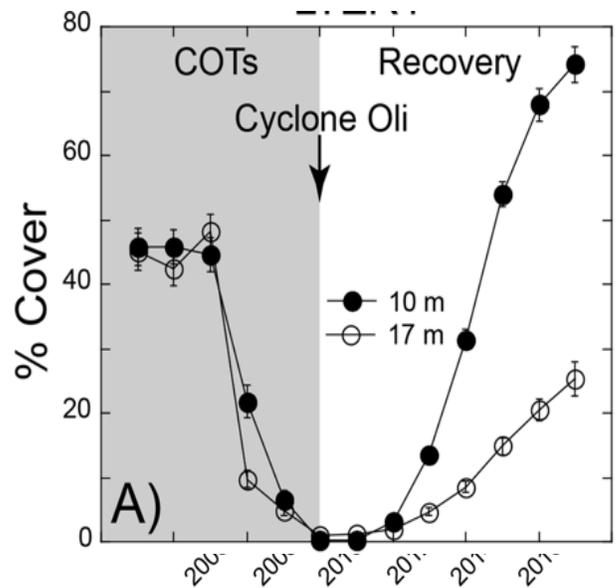


Figure 12.1. Corals declined dramatically from 2005-2010 as a result of increased grazing and cyclones before recovering between 2011-2017. The population density curve over time has the characteristic U-shape that is theoretically predicted under scenarios modeling evolutionary rescue (Gomulkiewicz and Holt 1995). Although the recovery cannot be definitively attributed to evolutionary rescue (rather than demographic rescue) without further genetic sampling, supporting data suggest that evolutionary rescue is the most likely explanation for the observed pattern (Edmunds 2018).

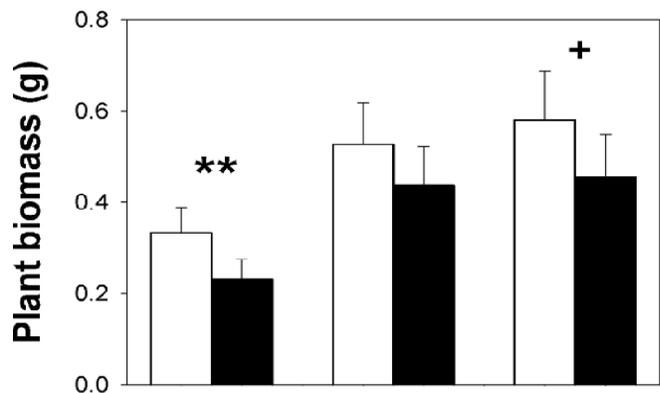


Figure 12.2. Twenty years of N-addition at the Kellogg Biological Station LTER has caused the evolution of less cooperative rhizobia. Plants inoculated with rhizobium strains isolated from long-term N-addition treatments (black bars) produced 17-30% less biomass depending on species, than plants inoculated from rhizobium strains isolated from nearby control plots (white bars) (Weese et al. 2015). Consistent patterns were observed across the three plant species tested (*Trifolium hybridum*, *T. pretense*, *T. repens*).

underlying this evolutionary response^{276,277} and suggests that even low levels of nitrogen addition select for less cooperative rhizobia. Other work finds that these evolutionary changes will influence community composition and soil N availability²⁷⁸. Repeated sampling at decadal intervals tests whether rhizobium quality will continue to decline and will allow researchers to investigate the genetic mechanisms involved in further evolutionary responses (e.g., mutations at the same genes identified in earlier studies or mutations at novel genes).

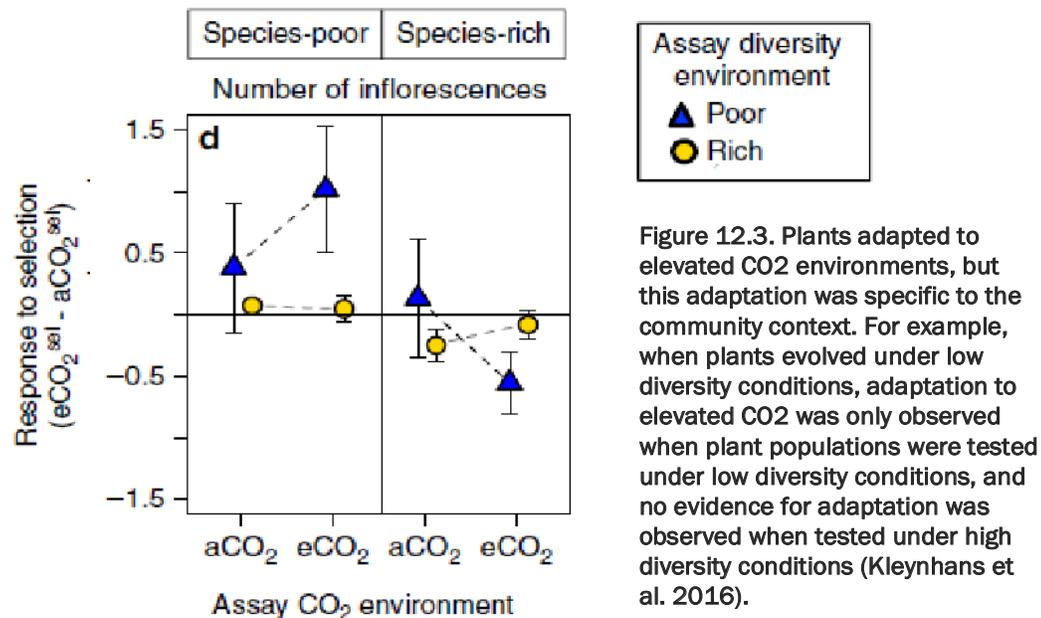


Figure 12.3. Plants adapted to elevated CO₂ environments, but this adaptation was specific to the community context. For example, when plants evolved under low diversity conditions, adaptation to elevated CO₂ was only observed when plant populations were tested under low diversity conditions, and no evidence for adaptation was observed when tested under high diversity conditions (Kleynhans et al. 2016).

While experimental evolution is often conducted in simplified lab environments²⁷⁹, adaptation in nature is much more complex, and theory predicts that the community context will alter evolutionary outcomes^{280,281}. An elegant study in a long term experiment manipulating species richness, atmospheric CO₂ concentrations, and nitrogen (BioCON) at CDR suggests that adaptation to the abiotic environment is specific to the community context²⁸². In other words, adaptation to elevated CO₂ was only observed when the test conditions (low vs. high plant species richness) matched the evolutionary history conditions (low vs. high species richness) (Figure 12.3).

Adapting to elevated CO₂ concentrations in low species richness treatments failed to confer adaptation to elevated CO₂ in high species richness treatments. These results are among the first to link community ecology with evolutionary responses to global change.

Decomposition is a central process to carbon cycling, and researchers at Harvard Forest have shown that in addition to shifting the community composition of fungal decomposers, N-addition also has caused several taxa within the fungal community to evolve reduced decomposition rates²⁸³, illustrating the feedbacks that can occur between evolution and ecology. The realization that rapid evolutionary responses could affect classic ecological patterns spawned the field of eco-evolutionary dynamics: that evolutionary responses can shift ecological interactions in ways that feedback to cause further evolutionary change^{284,285}. Quantifying eco-evolutionary feedbacks requires either archiving and comparing longitudinal samples (evolved vs. non-evolved populations) or comparing populations that have diverged among treatments²⁸⁶. LTER sites often can or do meet both of these

criteria and combined with their long history of measuring ecosystem function, also provide relevant ecological metrics and contexts, a key gap in existing eco-evolutionary work that is predominantly conducted in laboratory or mesocosm settings²⁸⁷.

Leveraging LTER experiments to study evolution is a relatively new endeavor, and the greatest contributions of LTER to the study of evolution have yet to be realized. We highlight three areas in which the LTER Network has great potential to make unique contributions to the study of evolution:

1. Despite long-standing recognition that ecology and evolution are interconnected^{288,289}, the fields of ecology and evolution have developed largely independently. Many of the forces and variables most commonly studied by community ecologists or ecosystem ecologists (e.g., eutrophication and disturbance) have received little attention in evolutionary biology, despite the fact that they are likely to be strong selective agents. For example, theoretical work posits that soil nitrogen should be a key driver of the evolution of resource mutualisms and plant defenses, and that disturbance should alter the evolution of dormancy and other life history parameters. LTER long term experiments manipulating both nitrogen and disturbance could test these classic theories.

2. The repeatability of evolution and how the genetic architecture of a population or particular ecological trade-offs in a given community constrain or alter evolutionary trajectories are fundamental questions being actively pursued by evolutionary biologists²⁹⁰. Because many experimental treatments are replicated across the LTER Network, the same species may experience selection by a particular treatment in very different contexts. Evolutionary studies conducted on common species across multiple sites could help illuminate the repeatability of evolution in nature and the potential constraints that may limit adaptation in some populations but not others. Several sites are taking the first step in this direction. A cross-site study involving Baltimore Ecosystem Study, Plum Island Ecosystem, Florida Coastal Everglades, Cedar Creek, and Central Arizona-Phoenix is taking

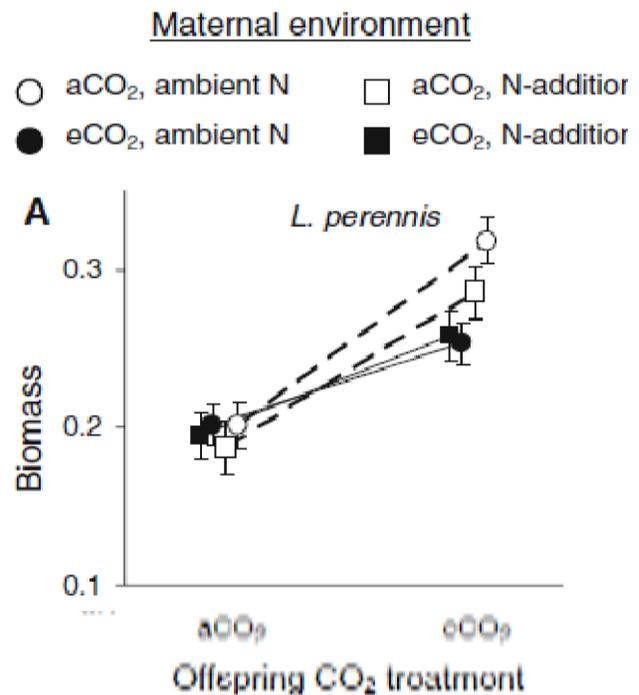


Figure 12.4. Evolving for 5 years in elevated CO₂ environments at CDR significantly reduced offspring growth responses to elevated CO₂. Although the authors did not control for maternal effects, if the observed responses are primarily due to genetic changes in ambient vs. elevated CO₂ populations, then evolutionary responses to elevated CO₂ may contribute to the attenuating responses to elevated CO₂ commonly observed over time in long-term experiments (Lau et al. 2008).

advantage of the idea that urbanization constitutes a natural experiment to study evolutionary mechanisms of adaptation^{215,291,292}.

3. Finally, given that evolution can occur exceptionally rapidly, it has the potential to influence ecological effect sizes²⁹³. If a goal of long term experiments is to predict natural population responses to environmental change, then considering evolution may be necessary for accurate predictions and may also explain some of the changing effect sizes observed over time in many long term experiments²⁹⁴ (Figure 12.4).

13 Information Management in the U.S. LTER Network

Effective long-term management and timely access to data emerging from LTER research has been a cornerstone of the LTER Network since its inception. LTER information managers had major roles in many of the ecoinformatics advances that underlie the FAIR Data Principles (Findable, Accessible, Interoperable, and Reusable) that we hear so much about today.

- LTER information managers have been involved in both the initial development and continued improvement of the Ecological Metadata Language (EML). EML – its granularity and network-wide adoption – is a cornerstone of the priorities established by the Network in service of accessible, reusable, and importantly, interpretable data.
- LTER information managers developed the concept of congruence checking²⁹⁵, which is the automated checking of metadata completeness and data-metadata consistency.
- A network wide controlled vocabulary contributes significantly to data search and discovery success^{296,297}.
- LTER working groups on management of streaming sensor data and geographic data began applying consistent practices well before “big data” became a watchword.

The LTER data repository infrastructure (PASTA)²⁹⁸ was already conceived, but not yet developed, at the time of the last decadal review in 2010, so reviewers’ recommendation that the Network would benefit by *‘markedly expanding its current data activities into a fully functional data management system that serves and archives all LTER data and metadata from all sites in a consistent and easily used manner to third-party users’*²⁹⁹ struck a sensitive chord. Software developers at the Network Office and site information managers completed development of the infrastructure and took the repository live in 2013.

With the launch of the LTER data repository – and to an even greater degree with the establishment of the Environmental Data Initiative (EDI) in 2016 – the Network’s vision of “a scientific community where information management contributes to long term data stewardship to support scientific research”³⁰⁰ is being realized at the level of the Network and the broader ecological community as well as at the site level.

The LTER repository, which is now maintained by the Environmental Data Initiative (EDI), is internationally recognized by many scientific journals as trustworthy, and holds important data products in support of publications and as well as irreplaceable long term data without which many current synthesis efforts would not have been possible³⁰¹⁻³⁰⁵. As of February 2019, it provides access to a total of 68,511 data packages. Of the data packages in the repository, 76% are from early, one-time LTER-wide efforts; namely, the EcoTrends synthesis project²⁰⁴ and Landsat imagery acquisitions. 16,742 dataset packages (24% of repository holdings, and including all revisions) were contributed by LTER site information managers representing nearly 2,300 individual data authors (Table 13-1).

Table 13-1. Number of unique data packages contributed by LTER sites as of April 30, 2019.

Site Data Packages					
Site	Data Packages	Site	Data Packages	Site	Data Packages
knb-lter-and	122	knb-lter-gce	595	knb-lter-nin	10
knb-lter-arc	655	knb-lter-hbr	174	knb-lter-ntl	260
knb-lter-bes	163	knb-lter-hfr	316	knb-lter-nwk	4
knb-lter-ble	1	knb-lter-jrn	104	knb-lter-nwt	248
knb-lter-bnz	583	knb-lter-kbs	70	knb-lter-pal	77
knb-lter-cap	198	knb-lter-knz	120	knb-lter-pie	464
knb-lter-cce	71	knb-lter-luq	170	knb-lter-sbc	207
knb-lter-cdr	516	knb-lter-mcm	279	knb-lter-sev	187
knb-lter-cwt	228	knb-lter-mcr	73	knb-lter-sgs	105
knb-lter-fce	172	knb-lter-nes	1	knb-lter-vcr	238

LTER's and EDI's approach to scientific data management and stewardship subscribes to the framework of the FAIR data principles, which are now widely adopted by the repository, data curation, and scientific publishing communities^{306,307} ([List of Signatories](#)³⁰⁸). FAIR principles serve as benchmarks: LTER data are *Findable* (in the [LTER data portal](#), and [Google Dataset search](#)) because they reside in an open repository, with unique and persistent identifiers and standard metadata indexed as a searchable resource; they are *Accessible* through industry standard protocols and are, in most cases, under an open-access license (access control is available if required); *Interoperability* is achieved by archiving data in commonly used file formats, and both metadata and data are machine readable and accessible; rich, high quality science metadata in EML format, render data fit for *Reuse* in multiple contexts and environments, along with easily generated data provenance to document their lineage.

The LTER Information Management Committee (IMC), includes one or more information managers from each site and meets monthly via videoconference to develop and share best practices and organizational updates. The committee holds an annual in-person meeting, often in association with a national conference, such as Earth Science Information Partners or the Ecological Society of America, which is invaluable for building a network of colleagues with similar roles and challenges.

The Information Management Committee, the Environmental Data Initiative and the LTER Network Office have established strong working relationships with distinct responsibilities, but shared goals and frequent communication.

- EDI closely collaborates with LTER information managers, continues the stewardship of published LTER data, and makes them findable and accessible to environmental researchers. Furthermore, EDI serves the larger ecological research community's data management and archiving needs³⁰⁹ by promoting the availability of data, and providing training in data management, search, and efficient use as well as data management services.

- LTER information managers facilitate the process of getting clean, reliable, usable data from field, to lab, to repository. They develop data cataloguing systems to meet the sites' needs, provide site-based training and services, work with synthesis groups to analyze and document data, and work (often in concert with EDI) to spot potential challenges on the horizon and develop systems for handling additional types of data (e.g. the current non-tabular data working group and the Zotero working group that is developing best practices for reference management).
- The LTER Network Office stewards the synthesis group development and selection process, supports virtual and in-person meetings, and other forms of collaboration, and ensures that synthesis-derived products are appropriately archived. The LNO also maintains current records of LTER participants, sites, and products, with the assistance of site-based information managers and administrators.

The quality of LTER data and metadata is often touted and a recent analysis (Gordon and Haberman, 2018 and Gordon et al. 2019), backs up the assertion with two major advancements attributable to the work of LTER information managers over the past decade: (1) the number of new and updated data package contributions per year and (2) the completeness of metadata relative to 25 general metadata concepts supporting FAIR principles. Both metrics have increased for all LTER sites over the last 10 years (Gordon et al. 2019). The analysis shows a metadata completeness of 75-80% for most LTER sites, which is approaching a maximum, because not all data require all categories of metadata. Moreover, in the same analysis LTER metadata completeness scored highest in most categories compared to ~40 other repositories in the DataONE network ³¹⁰.

While having data in accessible repositories is important, the real proof of value is data use. EDI monitors data download activity on a regular basis. The monthly average of data downloads for all LTER sites is 1,009 data files and most downloads are via automated workflows that are likely related to broader research efforts. (Internet robots are excluded from the measured data download rate.)

Perhaps the greatest recognition is evidence of data reuse — attribution of the dataset within a peer-reviewed scientific article. Data packages in the LTER Data Repository have received digital object identifiers (DOIs) since 2013 and now appear in literature. The culture of scientific publishing is now making data citation much more common, if not yet universal. In April 2019, a query to Google Scholar returned ~400 records that mentioned at least one LTER DOI as citation or in data availability statements (Fig. 13-1).

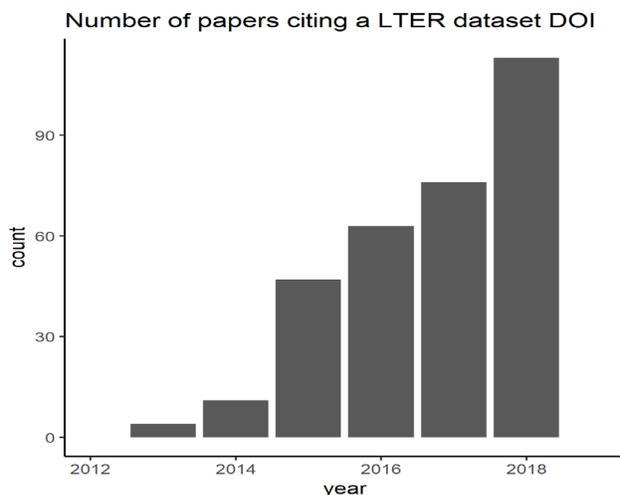


Figure 13.1. Number of papers citing at least one LTER dataset over time.

13.1 Broader impacts of information management activities

The early IMC annual meetings were among the first platforms for exchanging data management practices and experiences. Interest from outside the Network and requests to participate in the meetings motivated the organization of two larger Environmental Information Management Conferences^{311,312}.

A large body of publicly accessible software related to data management is available through the LTER version control systems. The IMC maintains a newsletter series called DataBits (<https://lternet.edu/tag/databits/>) in addition to publications in peer reviewed journals. Members of the US LTER have held leadership positions with ILTER and conducted workshops and training sessions across the globe³¹³.

In addition to developing an internationally recognized data repository with freely accessible and widely re-used data, the IMC has contributed to streaming sensor data management, offering several workshops, publishing extensively^{314,315}, and launching a broader community working group, now under the umbrella of the Federation of Earth Science Information Partners (ESIP, http://wiki.esipfed.org/index.php/EnviroSensing_Cluster).

13.2 Recent initiatives

In response to the second recommendation from the 30-year review that *'the LTER Network as a whole must invest in making LTER data comparable across sites'*²⁹⁹, EDI in collaboration with the LTER IMC has started several initiatives that will continue into the future.

A semantics working group is preparing for an upgrade of the LTER controlled vocabulary, possibly internationalizing it in collaboration with ILTER.

With several synthesis working groups focused on questions related to ecological communities, EDI personnel have started to bring long term ecological community observation data into a standard format that will facilitate future synthesis analyses. Additionally, the existing LTER climate database (climDB/hydroDB) will be upgraded to include higher frequency data and modern technology using a similar workflow framework. Both efforts will lead to LTER data becoming available to larger data harmonization efforts; e.g., climate-related data will be hosted by the Consortium of Universities for the Advancement of Hydrologic Science (CUAHSI) and community observations will be contributed to the Global Biodiversity Information Facility (GBIF).

Finally, the LTER IMC and the EDI repository are preparing to implement new features from the recently released EML 2.2 such as are found in data papers and standardized metadata content to further improve discovery and reuse potential.

In summary, the LTER IMC has risen to the challenge laid down in the 30-year review by developing a series of modular and flexible tools and practices to document, quality check, and share highly diverse ecological datasets. EDI is now expanding the use of those tools in a wide variety of other programs and engaging with the scholarly publishing community to assess the use and impact of ecological data.

14 Education and Outreach in the U.S. LTER Network

LTER sites are often located in well-preserved ecosystems that are characteristic of the region where they are located. They frequently are operated in collaboration with organizations that have an outreach or education mission and they are all teeming with multi-generational cadres of scientists with passion for, and knowledge of, their systems. These characteristics make them especially well-suited to provide the experiences that entice, engage, and educate people of all ages. Site educators and site leaders feel the privilege and responsibility of this position and are committed to the work of training future scientists and responsible citizens, engaging younger children in nature and scientific inquiry, and informing adults and professionals about how ecosystems work and the ways they benefit society.

At the same time, the variable nature of LTER sites, spread across diverse and sometimes remote ecosystems, together with a focus on place-based education, has led to tailored outreach programs at each site. Depending on the type of research conducted, staff skills and interests, and the proximity (or lack thereof) to schools and population centers, a site often must choose among allocating limited resources to classroom engagement, citizen science projects, undergraduate research and mentoring, art-science collaborations, and engagement with resource managers and landowners. Despite nuances of research focus, accessibility, and funding challenges, several initiatives have emerged across sites, allowing the Network to form a community of practice that promotes the exchange of best practices and promises to improve education models and outreach impacts within and beyond the LTER Network.

Site-based initiatives are diverse and creative, drawing on the talents and interests of site educators and partners. They run the gamut from targeted curriculum development to installation art. A quick perusal of the attached site briefs will give readers a flavor of the immense variety of projects emerging from LTERs.

Network-level initiatives focus on themes where LTER is exceptionally well-placed to have national impact and where a critical mass of participating sites exists, providing a robust community of practice across institutions and sites.

14.1 REU Experiences

Research Experiences for Undergraduates (REUs) are one of the most promising avenues for engaging members of groups that have been underrepresented in science – if they encounter an environment that respects and values their experience and that makes the culture, values, and tools of science accessible. LTER sites have 2 modes of undergraduate experiences: 1) A few LTER sites have large cohorts of REUs and strong infrastructure for recruiting, onboarding, and mentoring, supported through REU site programs; 2) REU supplements provide funding for 2 REUs per site, but no additional resources for support. The Network Office and the Education and Outreach Committee are working to make the best practices and resources generated at REU sites available to REU mentors with “supplement” REUs through REU lunch chats, network-wide REU enrichment opportunities, and developing opportunities for sharing experiences between these two types of participants.

Individual sites and the Network Office work together to promote REU opportunities. Harvard Forest LTER has made exemplary progress on recruiting a diverse pool of applicants. Thanks to deliberate

recruiting partnerships, 16-20% of the 450 applicants that Harvard Forest receives annually come from groups traditionally underrepresented in science. Harvard Forest allow their applicants to request consideration by other LTER sites and generally serves as a model for building inclusive programming. Many sites share orientation and mentoring resources, and the Education and Outreach Committee is exploring options for making successful enrichment programming developed at individual sites available across the Network. There is strong interest in developing a cross-site REU program building on this foundation, but a specific proposal has not yet been developed. RET initiatives mirror the REU program, though cross-site supports may prove even more influential there than for REUs, as most sites are funded to support only one teacher per year.

14.2 Data Literacy

LTER data provides many examples of how to find, organize, clean, analyze and plot real data while also being accessible to even young students, who can easily grasp the meaning of changes in plant and animal populations, for example. The Data Nuggets program (developed at the Kellogg Biological Station LTER site) disseminates free classroom activities, co-designed by scientists and teachers and derived from authentic science research projects, that provide opportunities to look for patterns in the data and to develop explanations about natural phenomena using the scientific data from the study. LTER-derived data nuggets are now LTER-branded and can be identified as coming from the Network. Data Jams, in which middle schoolers combine data analysis with creative expression, are now hosted at four sites. The Luquillo and Sevilleta sites even co-host a virtual symposium in Spanish.

Through the Education and Outreach Committee, sites compare best practices for identifying and creating effective Data Nuggets and data literacy programs, as well as share information and resources on formal evaluation of Schoolyard programs. At the 2018 All Scientists' Meeting, education managers and information managers met together to explore ways to identify and promote specific datasets with strong educational potential in the EDI portal. Discussion about how to archive and promote long term datasets collected by student visitors, citizen scientist and volunteers is also on-going.

14.3 Engagement with Ecosystem Managers

Almost every LTER site has found opportunities to engage with stakeholders by identifying and sharing the evidence base for management and planning. Through fact sheets and programs for agricultural professionals, Kellogg Biological Station LTER has been a model of stakeholder engagement. Sites also make relevant data available through decision support tools like that developed by Virginia Coast Reserve LTER for coastal resilience planning. At Hubbard Brook and Harvard Forest LTERs, outreach teams are working to understand scientists' goals for engagement, their attitudes and beliefs about engagement, and obstacles to engagement, funded by a grant through NSF's Advancing Informal Science Learning program. Investigators are now in the process of developing a new, broader proposal to include more sites.

15 Site Briefs

- 15.1 H.J. Andrews Experimental Forest LTER
- 15.2 Arctic LTER
- 15.3 Baltimore Ecosystem Study
- 15.4 Beaufort Lagoon Ecosystems LTER
- 15.5 Bonanza Creek LTER
- 15.6 Central Arizona-Phoenix LTER
- 15.7 California Current Ecosystem LTER
- 15.8 Cedar Creek Ecosystem Science Reserve LTER
- 15.9 Florida Coastal Everglades LTER
- 15.10 Georgia Coastal Ecosystems LTER
- 15.11 Hubbard Brook LTER
- 15.12 Harvard Forest LTER
- 15.13 Jornada Basin LTER
- 15.14 Kellogg Biological Station LTER
- 15.15 Konza Prairie LTER
- 15.16 Luquillo LTER
- 15.17 McMurdo Dry Valleys LTER
- 15.18 Moorea Coral Reef LTER
- 15.19 Northeast U.S. Shelf LTER
- 15.20 Northern Gulf of Alaska LTER
- 15.21 North Temperate Lakes LTER
- 15.22 Niwot Ridge LTER
- 15.23 Palmer Station Antarctic LTER
- 15.24 Plum Island Ecosystems LTER
- 15.25 Santa Barbara Coastal LTER
- 15.26 Sevilleta LTER
- 15.27 Virginia Coast Reserve LTER



H.J. Andrews Experimental Forest LTER

Photo credit: U.S. LTER

The H.J. Andrews Experimental Forest (AND) LTER is located in the Cascade Range of Oregon, and consists of 6,400 ha of conifer forest, meadows, and stream ecosystems. This mountain landscape experiences episodic disturbances, including fires, floods, and landslides. The question central to AND LTER research is: How do climate, natural disturbance, and land use, as influenced by forest governance, interact with biodiversity, hydrology, and carbon and nutrient dynamics?

Andrews LTER research illuminates the complexity of native, mountain ecosystems such as: forest-stream interactions; roles of dead wood; and effects of forest harvest and disturbance on hydrology, vegetation, and biogeochemistry over multiple time scales. Andrews LTER research has also been central to informing regional and national forest policy. Future research will address ongoing change in streams, forests, climate, and governance.



Between 2008-2018:

106 investigators

50 institutions represented

122 graduate students



Forest

Principal Investigator:

Michael P. Nelson

Oregon State University

Est. 1980

Funding Cycle:

LTER VII

NSF Program:

Biological Sciences /
Division of Environmental
Biology



Key Findings

Disturbance produces multi-decadal legacies.

The fire regime at AND LTER was previously believed to be dominantly stand-replacing. However, three quarters of 124 post-fire sites had multi-age cohorts of plant species, indicating mixed severity fires over the past 400 years [Product 9]. Pre-disturbance understory plant species persisted for decades after clear-cut logging and broadcast burning, contrary to the theory that severe disturbance would eradicate understory species [5].

Forest succession following clearcut harvest.

Due to increased shading from forest regrowth, streams in recovering forest experience declining temperatures, despite a warming climate [2]. Site history is essential to correctly interpreting climate change response to such trends.

Newly recognized stream responses to

warming trends.

Cross-site comparisons reveal varying long term trends in nitrogen exports [1], and varying responses to warming trends [7]. Although theory predicts that streamflow should recover quickly after disturbance, paired watershed comparisons found decreases in summer flow (relative to undisturbed watersheds)

in regenerating post-harvest forests 25 to 45 years old [8].

Carbon storage responds to forest growth, mortality, and climate.

Old-growth forest-stream ecosystems store enormous amounts of carbon. Andrews LTER researchers found that forest biomass accumulated at relatively linear rates over a century – counter to theoretical predictions that biomass accumulation would slow during forest succession [6]. They also found that climate change related mortality at Andrews is low compared to other forests in the western U.S. [10] and that forest harvest reduced stream dissolved organic carbon flux for over 50 years. According to predictions, valleys may be buffered from increasing temperature [4], but a warming climate could also push old-growth forests to become net carbon emitters.

Biodiversity losses and gains.

The northern spotted owl, an iconic species in federal lands policy, continues to decline. Over 4,000 invertebrate species have been recorded at AND LTER since 1991. Native climate-sensitive bird species appear to be persisting, despite multi-decade warming, likely because old forests buffer micro-climate [3].



Synthesis

Networking networks. Andrews LTER co-led two workshops on the integration of LTER, NEON, and CZO, resulting in a manuscript on research that combined LTER core areas and NEON core measurements.

Inter-site biogeochemistry and hydrology.

Andrews LTER led efforts to collect and make available data on stream chemistry (StreamChem) and climate and hydrology (Clim/hydroDB). Andrews researchers also led the planning process for a cross-site vegetation database (Veg-E).

Arts and humanities. Researchers and outreach specialists at AND LTER are leaders in the LTER Network-wide effort to engage arts and humanities. They have organized workshops, collaborated on social science publications, created a website, and co-organized multi-site art exhibits at NSF and Ecological Society of America meetings.



Photo credit: Lina DiGregorio

Ecosystem response to climate change.

Andrews LTER researchers led an effort to analyze climate change and hydrologic response at LTER sites [7] and are assembling ecosystem responses to climate change from all 28 LTER sites.



Data Accessibility

Since 1983, AND LTER data have been collected, managed, and archived through the Forest Science Data Bank (FSDB), which includes all active and legacy databases. Data are archived in the FSDB and the LTER Data Portal. Hydro-climatological data is collected using a radio telemetry system, allowing over 50 million records per year to be streamed. Andrews LTER also co-led a series of network-wide meetings on environmental sensor management and helped initiate the EnviroSensing Cluster in the Federation of Earth Science Information Partners (ESIP).

Photo credit: Erika Zambello

Partnerships

U.S. Forest Service, Pacific Northwest Research Station | Willamette National Forest | Oregon State University, College of Forestry



Broader Impacts



Fostering connections with the arts. Andrews LTER's environmental arts and humanities program develops lasting relationships with writers, artists, and musicians. Andrews LTER researchers have hosted some of the leading voices in the field ([The Forest Log](#)), shared work in major literary outlets (e.g., the *Atlantic* and *Orion* magazines), and published a book, [Forest Under Story](#). The ongoing Andrews History Project is archiving 70 years of historic documents and 55 oral histories.

Engaging middle school students. Andrews LTER partners with the University of Oregon Environmental Leadership Program, The Pacific Tree Climbing Institute, and the U.S. Forest Service Pacific Northwest Research Station to offer a curriculum, Canopy Connections, that integrates science, art, and creative writing and gives students an opportunity to climb into the canopy of an old-growth forest.

The Andrews Schoolyard LTER Program. A total of 84 K-12 teachers have worked with over 8,000 students per year in a program based on long term relationships with K-12 teachers and data from AND LTER.

LTER - Forest Service collaboration. For decades, scientific research at AND LTER has both influenced and been influenced by forest and stream management through joint field trips, symposia, and shared experiments.



Forest governance has changed. History and social science studies describe a long term change in forest management from a top-down governance system to one driven by local, bottom-up decision making. Pathways for science input to this new structure are less clear.

Photo credit: U.S. LTER

Top Products

1. Argerich, A and Johnson, SL et al. 2013. Trends in stream nitrogen concentrations for forested reference catchments across the USA. **Environmental Research Letters**. doi: 10.1088/1748-9326/8/1/014039
2. Arismendi, I and Johnson, SL et al. 2012. The paradox of cooling streams in a warming world: Regional climate trends do not parallel variable local trends in stream temperature in the Pacific continental United States. **Geophysical Research Letters**. doi: 10.1029/2012GL051448
3. Betts, MG et al. 2018. Old-growth forests buffer climate-sensitive bird populations from warming. **Diversity and Distributions**. doi: 10.1111/ddi.12688
4. Daly, C et al. 2010. Local atmospheric decoupling in complex topography alters climate change impacts. **International Journal of Climatology**. doi: 10.1002/joc.2007
5. Halpern, CB and Lutz, JA. 2013. Canopy closure exerts weak controls on understory dynamics: A 30-year study of overstory-understory interactions. **Ecological Monographs**. doi: 10.1890/12-1696.1
6. Harmon, ME and Pabst, RJ. 2015. Testing predictions of forest succession using long-term measurements: 100 yrs of observations in the Oregon Cascades. **J Veg Sci**. doi: 10.1111/jvs.12273
7. Jones, JA et al. 2012. Ecosystem processes and human influences regulate streamflow response to climate change at long-term ecological research sites. **BioScience**. doi: 10.1525/bio.2012.62.4.10
8. Perry, TD and Jones, JA. 2017. Summer streamflow deficits from regenerating Douglas-fir forest in the Pacific Northwest, USA. **Ecohydrology**. doi: 10.1002/eco.1790
9. Tepley, AJ et al. 2013. Fire-mediated pathways of stand development in Douglas-fir/western hemlock forests of the Pacific Northwest, USA. **Ecology**. doi: 10.1890/12-1506.1
10. van Mantgem, PJ et al. 2009. Widespread increase of tree mortality rates in the western United States. **Science**. doi: 10.1126/science



Arctic LTER

Arctic (ARC) LTER uses long term monitoring and manipulations of temperature, nutrient inputs, and community structure to understand how tundra terrestrial, stream, and lake ecosystems respond to climate change and climate-induced disturbances such as wildfire and permafrost thawing. Recent research explores biogeochemical and community openness and connectivity as ways to describe and predict how climate related changes propagate across the landscape.



Key Findings

Ecosystem enrichment in terrestrial and aquatic systems. Warming will increase nutrient cycling in soils, increasing its fertility and nutrient supplies to streams and lakes. Data from long term fertilization studies at ARC LTER are used to model tundra responses to climate change and disturbance. Long term phosphate fertilization has altered the Kuparuk River's structure and function, but lake response to fertilization is complicated by lake morphometry – benthic and planktonic communities exhibit different responses in deep versus shallow lakes.

Between 2008-2018:

33 investigators

21 institutions represented

20 graduate students



Tundra

Principal Investigator:

Edward B. Rastetter

The Marine Biological Laboratory

Est. 1987

Funding Cycle:

LTER VI

NSF Programs:

Biological Sciences / Division of Environmental Biology
Geoscience / Office of Polar Programs



Diversity of species interactions in a changing Arctic.

Microbial communities decreased from soil, to streams, to lakes. About half of the common lake bacteria detected were rare species in soils and headwater streams [Product 3]. Initial inoculation from soils was followed by species sorting downslope. With warming, microbial trophic structure has become more homogenous across soil horizons, and plant biomass and woody plant dominance has increased

[10]. Arctic LTER researchers have found that, in lakes, warming caused fish populations to cycle between large and small individuals. Models predicted faster growth, which would require more food, increased reproduction, and decreased generation time [1].



Transport and transformation of DOC in aquatic systems.

Dissolved organic carbon (DOC) released from thawing permafrost soil can be respired by microbes almost twice as fast if the DOC is first exposed to UV light [2]. Arctic LTER long term data indicate that direct photochemical degradation of DOC from land is the dominant mechanism of DOC oxidation in streams and lakes.

Indirect indicators of rapid warming in the Arctic.

Although air temperature at Toolik Lake is too variable for a warming trend to be statistically significant, several long term measures indicate warming [5]. After 40 years, satellite data indicate “greening,” but plot re-harvesting in 2018 does not indicate an increase in shrub abundance. Alkalinity in Toolik Lake has doubled over 40 years, indicating deeper thaw, which allows water to flow through from deeper, more carbonate-rich soil layers. Stream water alkalinity, base cation concentrations, nitrate, and DOC have all increased in ways consistent with permafrost thaw [6]. Dissolved phosphorus has decreased in the Kuparuk River, contrary to expectations.



Wildfire and thermokarst: impacts and recovery.

In 2007, a massive tundra fire released ~2 Pg of carbon into the atmosphere [8]. Climate-driven fire may accelerate warming, potentially offsetting the effects of arctic greening. Long term effects of wildfire on tundra were assessed and incorporated into a model simulating recovery from fire and the loss of ~66 Gg of nitrogen. Tundra darkening caused by fire likely increases thermokarst activity, increasing long term nutrient delivery to streams, and enhancing the biogeochemical connectivity between terrestrial and aquatic ecosystems. The magnitude of this effect is comparable to the ARC LTER fertilization experiments on the Kuparuk River.



Synthesis

An Arctic model of carbon metabolism. As part of the International Tundra Experiment (ITEX), ARC LTER scientists helped identify a convergence in ecosystem carbon metabolism among all major vegetation types in Arctic and subarctic tundra in Alaska, Greenland, Svalbard, and Sweden [9]. A single regression model predicts net ecosystem metabolism (NEP) as a function of leaf area, air temperature, and light. As the Arctic warms, biomass increases, and vegetation patterns shift — NEP can still be predicted based on these three easily quantified variables.

Forty-five years of tundra research. Research at Toolik Station began in 1975; a new book synthesizes research and results up to present day, emphasizing the importance of long term data measurements and curation through

LTER [5]. The volume includes chapters on past and predicted future climate, a synthesis of paleoenvironmental change in the ARC LTER region, and the ITEX collaboration.

Modeling nutrients and disturbance. The multiple element limitation (MBL MEL) model has been used to compare model predictions to five years of eddy covariance data from fire recovery with the aim of projecting long term tundra recovery from fire, and to spatially predict C, N, and P budgets for Northern Alaska. Arctic LTER researchers are identifying patterns of variation in response to climate and disturbance by applying the model to 8 LTER sites (ARC, AND, BNZ, HBR, KBS, KNZ, HFR, & NWT), an Amazonian tropical forest, and a pine plantation in the southeastern U.S.

Partnerships

Toolik Field Station, Institute of Arctic Biology, University of Alaska, Fairbanks | Marine Biological Laboratory | University of Michigan | Townson University | University of Vermont | Utah State University | NASA



Data Accessibility

The Arctic LTER data archive includes datasets from the Toolik Lake site and collaborating projects back to 1975. Datasets are updated and added after documentation and quality checking (usually within 2 years). They are then posted to the Arctic LTER website and to the Environmental Data Initiative (EDI) data portal where they are available and licensed under a Creative Commons License. Data from projects supported by the NSF Office of Polar Programs (OPP) are uploaded to the Arctic Data Center upon PI request.

Broader Impacts

Sharing priceless experiments. Arctic LTER actively encourages other researchers, their students, and postdocs to conduct complementary studies using ARC LTER field sites, experiments, and data.

Polar journalists. Arctic LTER has hosted approximately 20 journalists through the Logan Science Journalism Program at the Marine Biological Laboratory.

Engaging communities and resource managers. Researchers from ARC LTER regularly offer talks and short courses for Alaskan Native communities at Anaktuvuk Pass, Kaktovik, and Barrow. They also provide briefings to the U.S. Bureau of Land Management, Arctic National Wildlife Refuge, Alaska Division of Natural Resources, Alaska Fish and Game, and North Slope Borough.

Plugging into an Arctic network. Two NSF REU students per year — and many other graduate and post-baccalaureate students — gain invaluable field work experience at ARC LTER.



K-12 education. Arctic LTER has hosted over 35 K-12 teachers and PolarTREC teachers who work directly with site scientists. The LTER schoolyard program engages K-12 students in Barrow, AK and works with the Environmental Literacy Program at Colorado State University.

Top Products

1. Budy, P and C Luecke. 2014. Understanding how lake populations of arctic char are structured and function with special consideration of the potential effects of climate change: a multi-faceted approach. **Oecologia**. doi:10.1007/s00442-014-2993-8
2. Cory, RM et al. 2014. Sunlight controls water column processing of carbon in arctic freshwaters. **Science**. doi:10.1126/science.1253119.
3. Crump, BC et al.; 2012. Microbial diversity in arctic freshwaters is structured by inoculation of microbes from soils. **International Society For Microbial Ecology Journal**. doi:10.1038/ismej.2012.9
4. Gough, L et al. 2016. Effects of long-term nutrient additions on arctic tundra, stream, and lake ecosystems: beyond NPP. **Oecologia**. doi: 10.1007/s00442-016-3716-0
5. Hobbie, JE and GW Kling (eds). 2014. Alaska's Changing Arctic: Ecological Consequences for Tundra, Streams, and lakes. **Oxford University Press**, New York, New York, USA
6. Kendrick MR et al. 2018. Linking permafrost thaw to shifting biogeochemistry and food web resources in an arctic river. **Global Change Biology**. doi: 10.1111/gcb.14448
7. Kendrick, MR et al. 2018. Disturbance, nutrients, and antecedent flow conditions affect macroinvertebrate community structure and productivity in an arctic river. **Limnology and Oceanography Special Issue: Long-term Perspectives in Aquatic Research**. doi: 10.1002/lno.10942
8. Mack, MC et al. 2011. Carbon loss from an unprecedented arctic tundra wildfire. **Nature**. doi: 10.1038/nature10283
9. Shaver, GR et al. 2013. Pan Arctic modelling of net ecosystem exchange of CO₂. **Philosophical Transactions of the Royal Society B**. doi: 10.1098/rstb.2012.0485
10. Sistla, SA et al. 2013. Long-term warming restructures Arctic tundra without changing net soil carbon storage. **Nature**. doi: 10.1038/nature12129



Baltimore Ecosystem Study LTER

Since 1998, the Baltimore Ecosystem Study (BES) LTER has worked to advance the understanding of urban areas by asking three key questions: 1) What is the spatial and temporal patch structure of ecological, physical, and socio-economic factors in the urban ecosystem? 2) What are the fluxes of energy, matter, and populations in patches of the urban ecosystem? 3) What are the choices people and organizations make that affect the urban ecosystem?



Baltimore LTER researchers have pioneered new theory and methods for characterizing urban ecosystems. Watershed biogeochemistry, ecological communities and sentinel species, and human environmental perceptions and behaviors have been the measurements of focus. The research team has established long term records of urban watershed hydrology and biogeochemistry, developed and applied novel instruments for urban social survey, and characterized change in multiple dimensions of urban biodiversity. Baltimore LTER educators and scientists work extensively with students and schools in Baltimore to help bring science into the classroom.

Between 2008-2018:

92 investigators

37 institutions represented

162 graduate students



Urban

Principal Investigator:

Emma J. Rosi

Cary Institute of Ecosystem Studies

Est. 1998

Funding Cycle:

LTER IV

NSF Program:

Division of Environmental Biology / Ecosystem Science



Key Findings

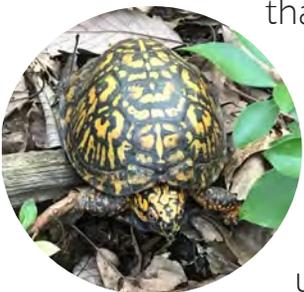
Pioneering urban system science. Researchers at BES LTER developed new theory [Product 2] and methods [5] for characterizing the multidimensional, multidisciplinary nature of urban ecosystems. This work sparked the development of a new “urban systems science” which has become a key component of sustainability science across the globe [7].

Understanding urban watersheds. Baltimore LTER research showed that nutrient cycling and retention in urban watersheds are driven by complex dynamics, with surprisingly high nitrogen retention, climate sensitivity, and surface water-groundwater interactions [1, 8]. These studies have been a foundation for novel analyses of how ecosystems are affected by contaminants of emerging concern [10].

Unexpected urban biodiversity. Baltimore LTER research has helped challenge the assumption that urban biodiversity is low by showing that biological communities in urban environments are diverse and dynamic. This diversity ultimately affects human well-being, and fluxes of water, energy, carbon, and nutrients [6, 9, 4].



Recognizing social feedbacks. The BES LTER Household Telephone Survey provided information on environmental knowledge, perceptions, values, and behaviors of residents, their influence on ecosystem structure and function, and the ways that ecosystem structure and function may affect residents’ physical activity, social cohesion, perception of neighborhood desirability, and willingness to relocate [3].



Synthesis

Urban homogenization. Baltimore LTER has a long history of collaboration with its sister site Central Arizona-Phoenix (CAP) LTER, including over 50 co-authored publications. Coordinated data collection (telephone survey, plant diversity, soil processes, microclimate, hydrography, plant and soil C and isotopes) began as part of two projects funded by the

NSF Macrosystems Biology program on “urban homogenization.” This work is ongoing, and has produced a series of direct comparisons between Baltimore and Phoenix, as well as comparisons with four other major U.S. cities: Boston, Miami, Minneapolis-St. Paul, and Los Angeles [6].

Partnerships

U.S. Forest Service, Baltimore Urban Field Station |
University of Maryland, Baltimore County



Photo credit: BES LTER

Data Accessibility

Baltimore LTER watershed data are the focus of outreach to local municipalities grappling with water quality regulations for the Chesapeake Bay via the Baltimore Urban Waters Partnership; these data along with the Baltimore LTER physical sample archive have attracted outside investigators to pursue new analyses. Core long term datasets on trace gases [8], biodiversity, and community perception surveys have facilitated cross-LTER site analyses [8] and research on urban homogenization [6].

Broader Impacts

Reaching urban schools. Since 2009, BES LTER has worked with 135 Baltimore teachers on a variety of education programs. One such project – Pathways to Environmental Science Literacy – involved 4 other LTER sites. Main outcomes included: 1) reaching thousands of students in Baltimore County and Baltimore City Public Schools (ca. 50% and 90% underrepresented minorities, respectively), 2) research on teaching and student learning, and 3) curricular modules on carbon, water, biodiversity, and citizenship.

Improving urban quality of life. Educators, researchers, and outreach specialists partner with government agencies, non-governmental organizations, communities, and neighborhoods to improve environmental quality and human health and well-being across the city using scientific research.

Engaging diverse youth in urban ecology. Since 2015, BES LTER has partnered with Parks and People Foundations

every summer to immerse a team of high school students in long term research through the BRANCHES Young Environmental Scientist Program.

Environmental Justice. Studies at BES LTER identified long term and institutionalized systems in Baltimore that perpetuate inequities over time. These findings inform the city's equity planning and serve as models for other U.S. cities.

High-resolution landcover mapping at BES LTER and urban tree canopy (UTC) data have contributed to national and international standards for urban landcover mapping. These data are required by the Maryland State Legislature for tracking canopy loss. They are also used by the City of Baltimore to analyze change and drivers of canopy change.



Photo credits: BES LTER (above map and cover photo)

Top Products

1. Bettez, N et al. 2015. Climate variation overwhelms efforts to reduce nitrogen delivery to coastal waters. **Ecosystems**. doi: 10.1007/s10021-015-9902-9
2. Grove, M et al. 2015. The Baltimore School of Urban Ecology: Space, Scale, and Time for the Study of Cities. **Yale University Press**, New Haven.
3. Hager, GW et al. 2013. Socio-ecological revitalization of an urban watershed. **Frontiers in Ecology and the Environment**. doi: 10.1890/120069
4. Swan, SM et al. 2017. Differential organization of taxonomic and functional diversity in an urban woody plant metacommunity. **Applied Vegetation Science**. doi: 10.1111/avsc.12266
5. Pickett, STA et al. 2017. Dynamic heterogeneity: a framework to promote ecological integration and hypothesis generation in urban systems. **Urban Ecosystems**. doi: 10.1007/s11252-016-0574-9
6. Groffman, PM et al. 2017a. Ecological homogenization of residential macrosystems. **Nature Ecology & Evolution**. doi: 10.1038/s41559-017-0191
7. Groffman, PM et al. 2017b. Moving towards a new Urban Systems Science. **Ecosystems**. doi: 10.1007/s10021-016-0053-4
8. Ni, X and PM Groffman. 2018. Declines in methane uptake in forest soils. **PNAS**. doi: 10.1073/pnas.1807377115
9. Schmidt, DJ et al. 2017. Urbanization erodes ectomycorrhizal fungal diversity and may cause microbial communities to converge. **Nature Ecology & Evolution**. doi: 10.1038/s41559-017-0123
10. Rosi-Marshall, E and T Royer. 2012. Pharmaceutical compounds and ecosystem function: An emerging research challenge for aquatic ecologists. **Ecosystems**. doi: 10.1007/s10021-012-9553-z



Beaufort Lagoon Ecosystems LTER

Photo credit: Susan Schonberg

The Beaufort Lagoon Ecosystems (BLE) LTER program focuses on productivity, trophic relationships, and biogeochemical cycling in the network of highly dynamic lagoons spanning Alaska’s northernmost coastline. Extreme seasonal variations in environmental conditions are the norm for Arctic lagoons. However, warming-induced changes may challenge the resilience of biotic communities that currently thrive there. Lagoons along the coast of Alaska’s Beaufort Sea support large populations of migratory waterfowl, fish, and marine mammals that are essential to the culture of Iñupiat communities in the region.



Research at BLE LTER investigates how temporal variations in terrestrial inputs and ocean exchange over seasonal, inter-annual, and inter-decadal periods affect these lagoon ecosystems. Focuses include factors affecting key species, the stability and resilience of microbial and metazoan food webs, and the role of lagoons near the land-sea interface as biogeochemical reactors and sources of greenhouse gases.

Note: The following entries include foundational work conducted during 2008-2018 that was essential to establishment of BLE LTER in August 2017.

At Present:

- 15** investigators
- 6** institutions represented
- 9** graduate students



Coastal

Principal Investigator:

Kenneth Dunton

University of Texas, Austin

Est. 2017

Funding Cycle:

LTER I

NSF Program:

Geosciences / Office of Polar Programs / Arctic Observing Network (AON)



Key Findings

Spring melt matters. Over half of the fresh water and water-borne nutrients flowing from land to the Alaska Beaufort Sea each year are delivered during a two-week period in the spring — earlier than most seasonal Arctic research begins. These inputs are dominated by three large rivers that flow into the central Alaska Beaufort Sea. The composition of nutrients in river water also varies markedly across Alaska's North Slope; proportions of inorganic versus organic nutrients in rivers feeding the Beaufort Sea increase with watershed steepness from west to east across the region. [Products 1, 2]

Diverse carbon sources fuel food webs. Most consumers in Beaufort Sea lagoons exhibit omnivorous (generalist) feeding strategies. Food web structure shifts with the seasons as food sources change from ice cover to open water. Multiple food sources provide sustenance to consumers including allochthonous (marine and terrestrial/riverine organic matter) and autochthonous (microphytobenthic and phytoplankton) organic matter. [3-6]

Coastal erosion is increasing. Consistent with reports from other regions of the Arctic and the Beaufort Sea Coast, coastal erosion rates appear to have increased along the shores of Elson Lagoon near Utqiagvik (formerly Barrow) over the last half century. Areas with historically low erosion rates are changing faster, but rates

do not exceed those of areas with historically high erosion. [7, 8]

Extreme variability in physio-hydrological conditions. Beaufort Sea lagoons experience large seasonal variations in temperature and salinity related to the Arctic freeze-thaw cycle. In the most extreme cases, lagoons swing from completely freshwater conditions during the spring to hypersaline conditions during the winter. Variations in salinity regimes among lagoons are modulated by ocean exchange characteristics and proximity to river mouths. Water transparency is highest during ice break-up, but following ice retreat, wind driven sediment resuspension increases light attenuation. [9,10]



Synthesis

Organic matter synthesis. The BLE LTER is participating in a network-wide synthesis of organic matter (OM) research on patterns and long term trends in OM pools and fluxes under ambient and experimental conditions. This cross-site effort also includes conceptual model development to support ongoing and future work on organic matter dynamics at LTER sites.

Ocean biogeochemistry model. This collaboration between BLE LTER and Northern Gulf of Alaska LTER scientists is focused on the development and application of a river inputs model for the area extending from the Alaskan Yukon to the Mackenzie River in Canada.



Photo credit: Ken Dunton

Partnerships

Arctic Refuge, U.S. Fish & Wildlife Service | Sandia National Laboratories | Belmont Forum | Arctic Domain Awareness Center | U.S.-International Tundra Experiment | NOAA-CREST center | Barrow Area Information Database | NEON | Polar Geospatial Data Center | USGS Alaska Science Center



**Sandia
National
Laboratories**

Data Accessibility

To ensure data accessibility, BLE LTER archives at the Environmental Data Initiative (EDI) and maintains replicate metadata with the Arctic Data Center. Beaufort LTER's online data catalog uses EDI's PASTA API to share archived datasets in real time. To support high quality metadata, BLE LTER maintains an internal data catalog using an EML-oriented design (created in partnership with other LTER sites), along with R scripts for generating EML from the database.

Broader Impacts

K-12 community and classroom engagement.

Since 2011, the Kaktovik Oceanography Program has connected K-12 summer science activities to formal lessons in the local public school. In addition, over 40 Iñupiat students annually are led in classroom and field activities by visiting scientists from diverse disciplines. Leveraged fund raising efforts have tripled LTER schoolyard funding.



Traditional knowledge (TK) panel.

Iñupiat hunters and fishers meet regularly with BLE LTER scientists to share local and traditional knowledge. Supported by Bureau of Ocean and Energy Management (BOEM) funding, this program helps inform both current and future scientific research aimed at benefiting the local community.

Outreach through art. Collaborations with artists, writers, and musicians have resulted in public interpretive dance performances and a

partnership with the Virginia Coastal Reserve LTER to produce a Coastal Futures Festival (Fall 2019).

Citizen science. Young community members collect samples and data seasonally to capture the critical transition from an ice dominated lagoon system to an open-water one. The goal is to support their role in the community as stakeholders and potential future scientists.



Photo credit: Ken Dunton

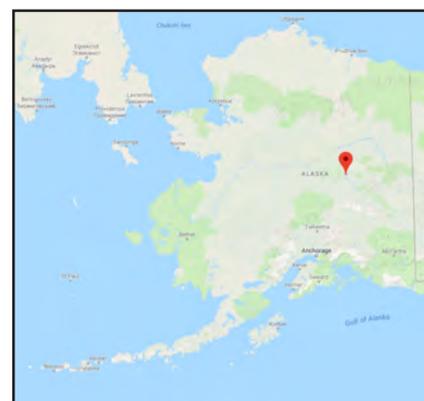
Top Products

1. McClelland, JW et al. 2014. River export of nutrients and organic matter from the North Slope of Alaska to the Beaufort Sea. **Water Resources Research**. doi: 10.1002/2013WR014722
2. Connolly, CT et al. 2018. Watershed slope as a predictor of fluvial dissolved organic matter and nitrate concentrations across geographical space and catchment size in the Arctic. **Environmental Research Letters**. doi: 10.1088/1748-9326/aae35d
3. Dunton, KH et al. 2012. Food Web Structure of the Alaskan Nearshore Shelf and Estuarine Lagoons of the Beaufort Sea. **Estuaries and Coasts**. doi: 10.1007/s12237-012-9475-1
4. Connelly, TL et al. 2015. Seasonal changes in quantity and composition of suspended particulate organic matter in lagoons of the Alaskan Beaufort Sea. **Marine Ecology Progress Series**. doi: 10.3354/meps11207
5. Mohan, SD et al 2016. Seasonal trophic linkages in Arctic marine invertebrates assessed via fatty acids and compound-specific stable isotopes. **Ecosphere**. doi:10.1002/ecs2.1429
6. Harris, CM et al. 2018. Do high Arctic coastal food webs rely on a terrestrial carbon subsidy? **Food Webs**. doi: 10.1016/j.fooweb.2018.e00081
7. Tweedie CE et al. 2012. Spatial and temporal dynamics of erosion along the Elson Lagoon Coastline near Barrow, Alaska (2002-2011). In Proceedings of the Tenth International Conference on Permafrost, Volume 1: International Contributions, Hinkel KM (ed). **The Northern Publisher: Salekhard, Russia**; 425-430
8. Jones, BM et al. 2018. A decade of remotely sensed observations highlight complex processes linked to coastal permafrost bluff erosion in the Arctic. **Environmental Research Letters**. doi: 10.1088/1748-9326/aae471
9. Harris, CM et al. 2017. Hydrology and geomorphology modulate salinity and temperature regimes in eastern Alaskan Beaufort Sea lagoons. **Estuaries and Coasts**. doi: 10.1007/s12237-016-0123-z
10. Bonsell, CE and KH Dunton. 2018. Long-term patterns of benthic irradiance and kelp production in the central Beaufort Sea reveal implications of warming for Arctic inner shelves. **Progress in Oceanography**. doi: 10.1016/j.pocean.2018.02.016



Bonanza Creek LTER

Bonanza Creek (BNZ) LTER is based in Alaska’s interior boreal forest, where the climate has warmed more than twice as rapidly as the contiguous U.S. over the past century. Bonanza Creek LTER research shows how climate warming has altered disturbance patterns and their interactions. Changes in fire frequency, size and severity, rate of permafrost thaw, surface hydrology, and insect and pathogen outbreaks are reshaping the Alaskan landscape by influencing biogeochemical cycles, succession, and patch size. Current research seeks to understand consequences for regional feedbacks to the climate system, and to identify social-ecological vulnerabilities, and to explore adaptation opportunities with rural Alaskan communities and land management agencies.



Data Accessibility

Since 1987, BNZ LTER has maintained a comprehensive catalog of data products. Data are submitted to the Environmental Data Initiative (EDI) repository, as well as to NASA, NADP, GenBank, and Ameriflux. A portal available to the streaming climate sensor network allows visitors to access and visualize current and historical measurements.

Between 2008-2018:

91 investigators

11 institutions represented

166 graduate students



Forest

Principal Investigator:

Roger Ruess

Institute of Arctic Biology,
University of Alaska, Fairbanks

Est. 1987

Funding Cycle:

LTER VI

NSF Program:

Biological Sciences
/ Division of
Environmental Biology



Key Findings

Severe fires drive shifts from black spruce to broadleaf dominance. Severe late summer fires consume the soil organic layer, allowing deciduous tree species, such as aspen and birch, to establish at high densities. The fast decomposing litter and rapid evapotranspiration of deciduous trees maintain a thinner, drier organic layer that does not sustain spruce forests or insulate permafrost. This ecosystem state change alters an iconic Alaskan ecosystem by modifying productivity and carbon storage, climate regulation, and other ecosystem services to society. [Products 1, 6]

Thawing permafrost and more frequent wildfires are likely to amplify climate warming to the same extent as land use change worldwide. Measurements across latitudinal gradients, field experiments, and laboratory incubations all point to significant releases of CO₂ and CH₄ from soils that have been frozen or waterlogged since the last ice age. Over decadal time scales, this carbon release could overwhelm increased plant carbon uptake. In a warmer world, the boreal forest could be transformed into a major carbon emitter, putting the forest on par with global land use change [10].



A longer snow free season is likely to increase energy absorbed by land surface and speed up warming.

Models that assess climate feedbacks over the next century have simulated decreases in albedo due to a shorter snow season, wider extents of deciduous forest due to altered fire regimes, and changes in climate and atmospheric CO₂ and CH₄ emissions. The strongest climate feedback was positive, derived from lengthening the growing season (reducing the snow-albedo feedback). Increases in young, faster-growing deciduous forests and a net increase in carbon uptake by terrestrial ecosystems only partially counterbalanced this change [3].

Browsing by large herbivores influenced vegetation development and ecosystem function. Browsing by moose and snowshoe hares affects plant species composition, growth, population dynamics, nutrient cycling, and ecosystem function at both stand and landscape scales, causing effects that can persist for decades. Both species selectively consume willows, leading to the dominance of alder, an important nitrogen-fixing species that is chemically defended against herbivory. Snowshoe hare abundance varies nearly as much on an intra-annual basis as it does across a decadal population cycle, underscoring the complex interaction of biophysical factors. This in turn influences predation intensity and the population abundance of lynx, which is largely controlled by emigration and immigration [4, 7].



Partnerships with local communities facilitate knowledge exchange. Local residents observe that warming has changed the timing of freeze up, affected river ice thickness and melt, and has reduced winter travel safety and access to local ecosystem services. Wildfire reduces access to the land, threatens cultural and historic sites, and reduces wildlife densities for one to several decades (e.g. moose and caribou, respectively). Sources of resilience range from oral traditions and cooperative harvesting strategies to new technologies and network sharing [2].



Synthesis

Forest regime change framework. Researchers at BNZ LTER led the development of a novel framework to articulate how changing disturbance regimes impact recovery and resilience of forest ecosystems. Two types of ecological memory (legacies) can support recovery, but may become misaligned with present conditions when disturbance regimes change, creating “resilience debt.” Information legacies include species adaptations and the pool of genetic information. Examples of material legacies include seed banks and soil carbon stores. Information from multiple diverse forest ecosystems indicates that they are most vulnerable to regime shifts when disturbance and climate change erode ecological memory. [Product 6]

Assessment of land carbon dynamics in Alaska. Bonanza Creek LTER helped design and execute the USGS assessment of carbon dynamics in Alaska, providing relevant information for climate policy and carbon management. The assessment provided information on: 1) feedbacks between ecosystem structure/function and fire regime 2) the fate of deep carbon in permafrost and

soils, and 3) the mass balance of carbon in and across uplands, wetlands, and surface waters in Alaska with a nominal 1 km² resolution. [8]

The Permafrost Carbon Network (PCN). Led by BNZ LTER scientists, the PCN links biological carbon cycle research to well developed networks in the physical sciences focused on the thermal state of permafrost. Partly supported by an NSF Research Coordination Network grant, the PCN produces new convergent knowledge to quantify how permafrost carbon drives climate change. [9]

Developing and applying social-ecological systems models. A community-based approach has led to a cross site comparison of the factors that mediate sensitivity to climate change, impacts on ecosystems and societies, and feedbacks from adaptive actions. This research has demonstrated that estimates of the future availability of ecosystem services are misleading if ecological factors are assessed in isolation. For example, in fishing, much of the variation in harvest effort is explained by fuel costs and policy rigidity, rather than fish stocks.

Broader Impacts

Citizen Science. Three BNZ LTER citizen science projects investigate the effects of longer growing seasons on boreal plant species, engaging over 1,800 volunteers of all ages. Together with Alaska GLOBE and dozens of international and train-the-trainer workshops, the impact of the program has grown to over 20,000 K-12 students.

Designing for diverse inclusion in research and education. Programs engage BNZ LTER scientists, teachers, youth, and indigenous knowledge holders in co-designing curricula. Features include cultural responsiveness, youth focused ecology research, access to subsistence food resources, and research on ecological change.

Integrating science education and social services. The Fostering Science program, started in 2017, brings scientists and youth in the care of the state together for a week long

“science adventure camp.” The program melds outdoor and science education with socio-emotional components designed to increase confidence, self efficacy, and resilience, and to cultivate interest in STEM careers.

Arts-humanities-science integration. In a Time of Change (ITOC), BNZ LTER’s place based arts-humanities-science program, has led to original public exhibits and performances. Themes include climate change, wildfire, predator control, and microbial worlds. Since 2008, ITOC events have involved dozens of artists and reached thousands of people.

Partnerships

U.S. Forest Service Pacific Northwest Research Station | University of Alaska, Fairbanks (UAF) | NEON



Top Products

- Alexander, HD and MC Mack. 2016. A canopy shift in interior Alaskan boreal forests: consequences for above and belowground carbon and nitrogen pools during post-fire succession. **Ecosystems**. doi: 10.1007/s10021-015-9920-7
- Brinkman, TJ et al. 2016. Arctic communities perceive climate impacts on access as a critical challenge to availability of subsistence resources. **Climatic Change**. doi: 10.1007/s10584-016-1819-6
- Euskirchen, ES et al. 2016. Consequences of changes in vegetation and snow cover for climate feedbacks in Alaska and northwest Canada. **Environmental Research Letters**. doi: 10.1088/1748-9326/11/10/105003
- Feierabend, D, and K Kielland. 2015. Seasonal effects of habitat on sources and rates of snowshoe hare predation in Alaskan boreal forests. **PLoS ONE**. doi: 10.1371/journal.pone.0143543
- Johnstone, JF et al. 2016. Changing disturbance regimes, ecological memory, and forest resilience. **Frontiers in Ecology and the Environment**. doi: 10.1002/fee.1311
- Johnstone, JF et al. 2010. Changes in fire regime break the legacy lock on successional trajectories in the Alaskan boreal forest. **Global Change Biology**. doi: 10.1111/j.1365-2486.2009.02051.x
- Kielland, K et al. 2010. Demography of snowshoe hares in relation to regional climate variability during a 10-year population cycle in interior Alaska. **Canadian Journal of Forest Research**. doi: 10.1371/journal.pone.0143543
- McGuire, AD et al. 2018a. Assessing historical and projected carbon balance of Alaska: A synthesis of results and policy/management implications. **Ecological Applications**. doi: 10.1002/eap.1768
- McGuire, AD et al. 2018b. Dependence of the evolution of carbon dynamics in the northern permafrost region on the trajectory of climate change. **PNAS**. doi: 10.1073/pnas.1719903115
- Schuur, EA et al. 2015. Climate change and the permafrost carbon feedback. **Nature**. doi: 10.1038/nature14338

Photo credits: BNZ LTER / U.S. LTER

Central Arizona–Phoenix LTER

As one of two sites in the LTER Network at the urban-wildland interface, understanding urban ecosystems has always been central to the Central Arizona–Phoenix (CAP) LTER enterprise. The 6,400 km² study site includes both the Phoenix Metropolitan Area and the outlying Sonoran desert. The central question at CAP LTER is focused on the interconnectedness of human and environment interactions: How do the ecosystem services provided by Urban Ecological Infrastructure (UEI) affect human outcomes and behavior, and how do human actions affect patterns of urban ecosystem structure and function and, ultimately, urban sustainability and resilience? For 22 years, CAP LTER researchers have explored social-ecological frontiers in interdisciplinary urban ecology through the study of residential landscapes, urban water bodies, desert parks and preserves, the flora, fauna, and climate of a riparianized desert city, and urban design and governance. Broader impacts of CAP LTER’s work include convergence research, with a theoretical focus on the nexus of ecology and design to enhance urban sustainability and resilience. A new theoretical focus for CAP LTER is UEI – a critical bridge between the system’s biophysical and human/social domains. The dynamics of UEI will guide research and activities for the next 5-10 years.



Between 2008-2018:

93 investigators

12 institutions represented

92 graduate students



Urban

Principal Investigator:
Daniel L. Childers
Arizona State University

Est. 1997
Funding Cycle:
LTER IV

NSF Program:
Biological Sciences /
Division of Environmental
Biology



Key Findings

Effects of the 2008 Great Recession on plant communities in residential landscapes.

Widespread loss of management (irrigation, weeding, planting, fertilizing) occurred when people were forced to leave their homes, driving an increase in post-recession plant species richness and community homogeneity as abandoned yards were taken over by weedy annual species [Product 7].

Urban Heat Island (UHI) research. Urban heat affects human health and well-being in many ways. Related impacts on human well-being will increase under most climate change scenarios.

Researchers at CAP LTER visualized spatial disparities in human-health impacts and environmental perceptions by combining remotely sensed temperature and land cover data at parcel and neighborhood scales with Phoenix Area Social Survey data [6].

Determining optimal irrigation regimes for mesic and xeric residential landscapes. Soil moisture dynamics were modeled using soil moisture data from the long term experimental landscapes at our North Desert Village experimental neighborhood. The relationship between irrigation schedules and plant stress differed by landscape type, which has implications for optimal irrigation regimes [9].

Plant mediated control of surface hydrology in a constructed wetland.

Plants at the Tres Rios constructed wastewater treatment wetland were found to be highly productive, transpiring large volumes of water, particularly in the hot, dry summer. A plant driven “biological tide” brings new water and nutrients into the marshes to replace these transpiration losses, making a treatment wetland more effective than if it were located in a cooler or more mesic environment [2].

Exploring the mechanisms that drive urbanization and its impacts on biotic diversity. An experiment that manipulated food resources and predation showed that different factors regulate plant-associated arthropod communities in desert and urban habitats. Bottom up factors were most influential in desert habitats, while urban arthropods responded to a complex set of relationships among climate, plant growth, and predation. Long term research at 12 riparian sites showed that engineered sites supported more generalists while native desert sites supported more specialists. Bird abundance, species richness, and diversity decreased across all riparian types from 2001-2015, and the riparian bird community is shifting towards one characteristic of more engineered sites with less water [1].





Synthesis

Urban homogenization. Central Arizona–Phoenix LTER is working with four other LTER sites to understand how urbanization tends to reduce the unique character of plant and animal communities in each location, making distant cities more biotically similar to each other.

Sharing and comparing with Baltimore Ecosystem Study LTER. There is a long history of collaboration and collegiality between CAP LTER and its companion urban LTER program in Baltimore, especially in the areas of scenarios research and ecology design nexus. Comparing results of the Phoenix Area Social Survey with the Baltimore Phone Survey, researchers at the two sites have related long term change in these social data to patterns of land cover change using high resolution (0.8 m) land use and land cover change data and socio-economic data from both cities.

Urban climatic extremes. The Urban Resilience to Extremes Sustainability Research Network (UREx SRN) integrates social, ecological, and technological systems to devise, analyze, and support urban infrastructure decisions in the face of climatic uncertainty. The foundation established by CAP LTER research was a key factor in basing this international network at Arizona State University.

Data Accessibility

Information management at CAP LTER is well developed; datasets are up to date and archived with the Environmental Data Initiative, documented, and publicly accessible. Central Arizona–Phoenix LTER is an active contributor to the LTER Network Information Management Committee. The Information Manager at CAP LTER works with scientists, students, and staff to address data management throughout the knowledge generating enterprise – from research design to data publication, including teaching a research data management methods course through ASU’s School of Sustainability.



Broader Impacts

Convergence research. Transdisciplinary and translational questions are an important component of the core research effort for CAP LTER. Social-ecological science – especially in cities – is particularly suited for this approach. Key goals include: 1) raising awareness of cities as social-ecological platforms for solving sustainability challenges and 2) co-producing knowledge with decision makers.

Spatially explicit, long term database on social-ecological variables. Researchers, city managers, and the public have access to CAP LTER's comprehensive database.

Education outreach at all levels. K-12 education through an award-winning Ecology Explorers program; 39 undergraduate students supported through a REU program; 58 graduate students funded since 2010 through our novel Grad Grants program; several postdocs funded.

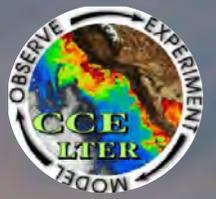
Partnerships

Arizona State University Decision Center for a Desert City (ASU DCDC) | Central Arizona Conservation Alliance | McDowell Sonoran Conservancy | The Nature Conservancy



Top Products

1. Bang, C et al. 2012. Control of arthropod abundances, richness and composition in a heterogeneous desert city. **Ecological Monographs**. doi: 10.1890/11-0828.1
2. Bois, P et al. 2017. Confirming a plant-mediated “Biological Tide” in an aridland constructed treatment wetland. **Ecosphere**. doi: 10.1002/ecs2.1756
3. Cook, EM et al. 2012. Residential landscapes as social-ecological systems: a synthesis of multi-scalar interactions between people and their home environment. **Urban Ecosystems**. doi: 10.1007/s11252-011-0197-0
4. Hale, RL et al. 2015. Stormwater infrastructure controls runoff and dissolved material export from arid urban watersheds. **Ecosystems**. doi: 10.1007/s10021-014-9812-2
5. Hall, J et al. 2011. Ecosystem response to nutrient enrichment across an urban airshed in the Sonoran Desert. **Ecological Applications**. doi: 10.1890/10-0758.1
6. Jenerette, GD et al. 2016. Micro-scale urban surface temperatures are related to land-cover features and residential heat related health impacts in Phoenix, AZ USA. **Landscape Ecology**. doi:10.1007/s10980-015-0284-3
7. Ripplinger, J et al. 2017. Boom-bust economics and vegetation dynamics in a desert city: How strong is the link? **Ecosphere**. doi: 10.1002/ecs2.1826
8. Shrestha, M et al. 2012. Land fragmentation due to rapid urbanization in the Phoenix Metropolitan Area: Analyzing the spatiotemporal patterns and drivers. **Applied Geography**. doi: 10.1016/j.ap-geog.2011.04.004
9. Volo, TJ et al. 2014. Modeling soil moisture, water partitioning, and plant water stress under irrigated conditions in desert urban areas. **Ecohydrology**. doi:10.1002/eco.1457
10. Zhang, C et al. 2013. A hierarchical patch mosaic ecosystem model for urban landscapes: Model development and evaluation. **Ecological Modelling**. doi: 10.1016/j.ecolmodel.2012.09.020



California Current Ecosystem LTER

Coastal upwelling biomes are found along the eastern margins of all major ocean basins, and represent some of the most productive ecosystems in the world ocean. The 193,000 km² California Current Ecosystem (CCE) LTER focuses on the planktonic food web, which is particularly responsive to climate forcing. Over 70 years of records from CCE LTER partner California Cooperative Oceanic Fisheries Investigations (CalCOFI) demonstrate that the California current food web is perturbed on multiple time scales by El Niño, multi-decadal oscillations, and an underlying warming trend.

Scientists at CCE LTER are addressing all of these time scales, focusing in particular on abrupt transitions in pelagic ecosystem state and the mechanisms that lead to such changes. California Current Ecosystem LTER integrates experimental process studies at sea, diverse autonomous and shipboard observational technologies, and coupled models.



Between 2010-2018:

43 investigators

30 institutions represented

57 graduate students



Marine

Principal Investigator:

Mark D. Ohman

Scripps Institution of Oceanography, UC San Diego

Est. 2004

Funding Cycle:

LTER III

NSF Program:

Geosciences /
Division of Ocean Sciences /
Biological Oceanography



Key Findings

Episodic and (sub)mesoscale features alter primary production and carbon export.

Process studies and related time series measurements reveal the under-appreciated importance of episodic events in the oceanic carbon budget. Spatial and temporal perturbations to the carbon cycle can be associated with (sub)mesoscale features (fronts, eddies, and filaments), which CCE LTER researchers have shown tend to be sites with enhanced phytoplankton and zooplankton biomass and production, and vertical carbon flux. [Products 3, 6, 10]

Iron supply broadly influences carbon dynamics. Iron supply in the CCE LTER region not only impacts carbon production and export associated with mesoscale circulation features. It also influences phytoplankton growth and species composition at the subsurface chlorophyll maximum layer (SCML), which is a widespread feature during spring and summer. Consistent with regional climate indices, biogeochemical proxies for iron

limitation revealed increasing frequency of iron

limitation at SCMLs in the California Current system.

These results are relevant to upwelling systems worldwide. [1, 6, 10]

El Niño and Warm Anomalies restructure the ecosystem.

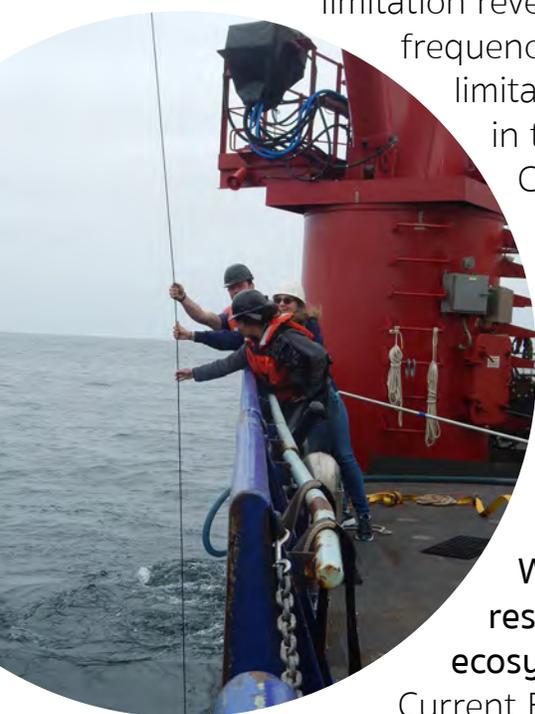
California Current Ecosystem

LTER researchers published

a cluster of 5 papers in *Deep-Sea Research* (vol. 140, Oct. 2018) that analyzed biotic responses to two successive perturbations of the California Current pelagic ecosystem: the Warm Anomaly of 2014-15 followed by El Niño of 2015-16. These studies drew on 12 years of LTER process studies and an analysis of 66-year records from CalCOFI to develop a quantitative basis for forecasting future responses of biotic processes including primary production, zooplankton community composition, and carbon export [2].

Double Integration of climate forcing. More than 60 years of zooplankton census data revealed that some populations respond indirectly to climate changes in two stages: first, ocean circulation responds to wind, then the zooplankton population level responds to ocean circulation. This broadly applicable principle of 'double integration' implies that direct correlations with climate variables should be replaced by metrics that reflect the biological time scale (e.g., life span) of the organisms concerned [9].

Optimized satellite remote sensing products. Several years of effort have led to an important California Current [merged satellite-derived 4 km dataset](#) becoming openly available online. The website provides access to regionally optimized remote sensing products and rigorously integrated time series for chlorophyll-a, net primary production, and export flux of carbon from 1996 to 2019.





Synthesis

ILTER EcoTrends project. Lead PI Mark Ohman was a member of the editorial board and co-author of 11 chapters in the LTER EcoTrends report, which summarized extensive climate and ecosystem time series across all U.S. LTER (and other) sites. Peters et al. (eds.) (2013) Long-Term Trends in Ecological Systems: A Basis for Understanding Responses to Global Change.

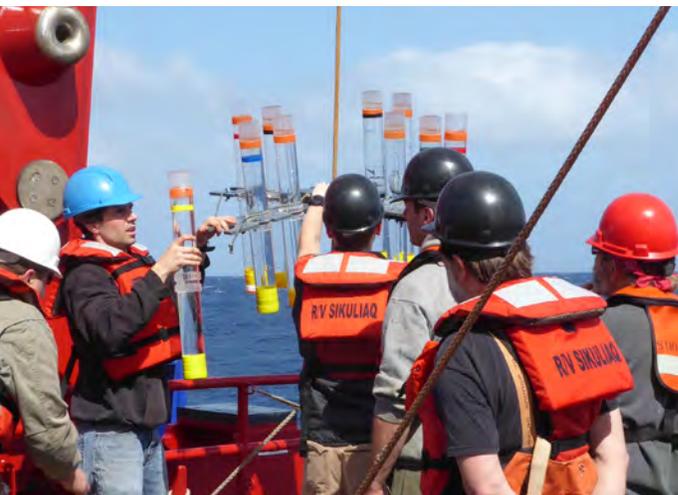
Integration of new pelagic sites into the LTER network. The LTER Network established 3 new marine sites in 2017. Investigators at CCE LTER organized meetings and workshops at scientific society meetings and LTER All-Scientists' Meetings, as well as informal data and methods exchanges.

Researchers from CCE LTER led an **international, pan-Pacific synthesis** of pelagic ecosystem responses to climate forcing: Di Lorenzo et al. 2013. Synthesis of Pacific Ocean Climate and Ecosystem Dynamics. Oceanography. 26: 68-81.



Partnerships

California Cooperative Oceanic Fisheries Investigations (CalCOFI) | Birch Aquarium | Scripps Institution of Oceanography (SIO) | SIO Pelagic Invertebrate Collection



Data Accessibility

Project and collaborator data (e.g. CalCOFI) are published through CCE LTER's local data catalog, Datazoo (documented according to LTER best practices). Datazoo archives new and updated datasets with the Environmental Data Initiative (EDI) through a single command. Other data are archived in appropriate repositories, such as NCEI (via R2R) for shipboard data.

Broader Impacts

Engaging the public at Birch Aquarium at Scripps. California Current Ecosystem LTER partners with Birch Aquarium, the public outreach center for the Scripps Institution of Oceanography, to support and deliver sustained outreach programming that incorporates research into exhibits and hands-on activities.

Professional Development for Teachers.

Professional development is delivered to teachers from local urban school districts. Drawing on LTER data and research methods, the program empowers teachers to provide authentic coastal ocean learning experiences.



Partnership with the private, non-profit Ocean Institute. Through a 14-year citizen science partnership with Ocean Institute, student volunteers collect and evaluate data while on educational programs, and share these data with CCE LTER scientists.

Undergraduate Opportunities. Undergraduate students are hosted by CCE LTER each summer via a REU program, which focuses on students from traditionally underrepresented groups and undergraduate-serving institutions.

Top Products

1. Hogle SL, et al. 2018. Pervasive iron limitation at subsurface chlorophyll maxima of the California Current. **PNAS**. doi: 10.1073/pnas.1813192115
2. Ohman MD. 2018. Introduction to collection of papers on the response of the southern California Current Ecosystem to the Warm Anomaly and El Niño, 2014–16. **Deep Sea Research Part I**. doi: 10.1016/j.dsr.2018.08.011 (5 papers).
3. Smith KL et al. 2018. Episodic organic carbon fluxes from surface ocean to abyssal depths during long-term monitoring in NE Pacific. **PNAS**. doi: 10.1073/pnas.1814559115
4. Taylor AG, Landry MR. 2018. Phytoplankton biomass and size structure across trophic gradients in the southern California Current and adjacent ocean ecosystems. **Marine Ecology Progress Series**. doi: 10.3354/meps12526
5. Biard T et al. 2018. The significance of giant phaeodarians (Rhizaria) to biogenic silica export in the California Current Ecosystem. **Global Biogeochemical Cycles**. doi: 10.1029/2018gb005877
6. Stukel MR et al. 2017. Mesoscale ocean fronts enhance carbon export due to gravitational sinking and subduction. **PNAS**. doi: 10.1073/pnas.1609435114
7. Lindegren M et al. 2016. Resilience and stability of a pelagic marine ecosystem. **Proceedings of the Royal Society of London Series B**. doi: 10.1098/rspb.2015.1931
8. Asch RG. 2015. Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. **PNAS**. doi: 10.1073/pnas.1421946112
9. Di Lorenzo E, Ohman MD. 2013. A double-integration hypothesis to explain ocean ecosystem response to climate forcing. **PNAS**. doi: 10.1073/pnas.1218022110
10. Landry MR et al. 2012. Pelagic community responses to a deep-water front in the California Current Ecosystem: overview of the A-Front Study. **Journal of Plankton Research**. doi: 10.1093/plankt/fbs025 (entire issue of 8 articles devoted to CCE-LTER's A-Front study).

Photo credits: CCE LTER



Cedar Creek Ecosystem Science Reserve LTER

Photo credit: Jabob Miller

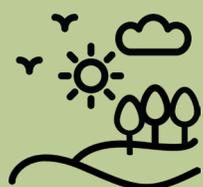
Cedar Creek Ecosystem Science Reserve (CDR) LTER in central Minnesota includes upland habitats – oak savanna, prairie, hardwood forest, pine forests, abandoned agricultural fields – and lowlands dominated by ash and cedar swamps, acid bogs, marshes, and sedge meadows. Early CDR LTER research developed theory and experiments to understand plant succession and nutrient limitation.



Currently, CDR LTER uses long term observations and experiments, theory, and models to understand two main concepts: 1) how ecological systems will respond to human-driven environmental changes that interact at multiple biological, spatial, and temporal scales, and 2) how ecological responses moderate or amplify environmental changes and how this may affect ecosystem services.

Between 2008-2018:

56 investigators
21 institutions represented
72 graduate students



Mixed Landscape

Principal Investigator:

Eric Seabloom

University of Minnesota

Est. 1982

Funding Cycle:

LTER VII

NSF Program:

Biological Sciences /
Division of Environmental
Biology



Key Findings

Soil resources jointly limit the response of grassland ecosystems to elevated CO₂. In two nested global change experiments, nitrogen (N) and soil moisture jointly constrained the response of biomass production to elevated CO₂ over the long term. When both water and N were limited, elevated CO₂ did not affect plant biomass. When neither resource was limited, elevated CO₂ caused an increase in plant biomass [Product 9].



Chronic N enrichment reduces plant biodiversity and alters plant community composition. Chronic N addition reduced plant species richness and led to the local extinction of species with efficient N use. Species richness returned to its original level after ceasing the addition of low levels of N. These changes in composition were readily reversed after low levels of N were no longer added. However, species richness did not recover two decades after ceasing the addition of high levels of N. Network-wide synthesis projects are testing how applicable this observation may be across different ecosystem types. [3, 6, 7]

Biodiversity increases ecosystem productivity and stability. Research in the 1990s demonstrated that more diverse herbaceous plant communities are more productive and exhibit less year-to-year variability in net primary productivity (NPP). Recently, this positive relationship has also been observed in forest communities. New

CDR LTER research also indicates that the relationship increases in strength with experiment duration in grasslands. Recent network-wide synthesis projects are scaling results up from biodiversity experiments to natural communities and testing predictions. [4, 5, 8, 10]

Photo credits: Frank Menschke (top); Jacob Miller (middle, bottom)

Partnerships

University of Minnesota (UMN)
College of Biological Sciences | UMN
Office for the Vice President for
Research



Synthesis

Lead and participate in observational networks and coordinated experiments.

Several networks focus on nutrient manipulation (Nutrient Network), drought (DroughtNet), and tree diversity (IDENT), as well as Urban Homogenization and Yard Futures studies. In particular, the Nutrient Network experiment is demonstrating that work conducted at CDR LTER for herbaceous ecosystems can be generalized worldwide [1].

Founding members and contributors to numerous global ecological databases.

Cedar Creek LTER scientists have led and participated in many global syntheses that used databases such as the TRY plant trait database, the ART-DECO decomposition database, the FRED root database, and the EcoSIS spectral library. Each examines relationships among traits and trait effects, and how these affect ecosystem function.

Cedar Creek LTER leads efforts in biodiversity remote sensing. Long term experiments, including grassland and forest biodiversity experiments, the savanna fire frequency experiment, global change experiments, and old field succession experiments, have served as key test beds for developing approaches to remotely sensing biodiversity and linking it to below ground processes [2].



Data Accessibility

Over 500 actively curated datasets (some extending back 80+ years) are made accessible, stored in a central database at the University of Minnesota, backed up off site, and synchronized with the Environmental Data Initiative (EDI) data catalog. Cedar Creek LTER also supports critical information management for the Nutrient Network.

Photo credits: U.S. LTER (top, bottom); Peter Wragg (middle)

Broader Impacts



Building pathways to lifelong science learning.

Participants build long term relationships with the landscapes, people, and science at CDR LTER through in-school programs (grades K-3), guided field trips (4-7), student-driven investigations (8-12), independent research projects (undergraduates), and citizen science projects (adults and families). These programs reach over 12,000 participants annually.

Community members contribute to long term science. Through three citizen science projects (Red-headed Woodpecker Project, Cedar Creek Wildlife Survey, and Eyes on the Wild) over 5,000 volunteers from around the world assist in wildlife studies. They monitor

woodpeckers, document tracks and sign, and identify and characterize animals in trail camera images on a web interface. Data from these projects fill gaps in CDR LTER's work on wildlife and help researchers maintain records of animal populations, distribution, and relative abundance.

Connecting graduate students and middle school students. Two programs guide 25 graduate students in mentoring approximately 700 7th and 8th grade students to develop questions, collect and analyze data, and present findings to their peers.

Artists in Residence. Each year, several artists work closely with CDR LTER researchers, students, and staff to interpret and represent key experiments and landscapes. Public showcases engage a statewide audience.



Photo credits: Caitlin Potter

Top Products

1. Borer, ET et al. 2014. Herbivores and nutrients control grassland plant diversity via light limitation. **Nature**. doi: 10.1038/nature13144
2. Cavender-Bares, JJ et al. 2017. Harnessing plant spectra to integrate the biodiversity sciences across biological and spatial scales. **American Journal of Botany**. doi: 10.3732/ajb.1700061
3. Clark, CM and D. Tilman. 2008. Loss of plant species diversity after chronic low-level nitrogen deposition to prairie grasslands. **Nature**. doi: 10.1038/nature06503
4. Grossman, JJ et al. 2017. Species richness and traits predict overyielding in stem growth in an early-successional tree diversity experiment. **Ecology**. doi: 10.1002/ecy.1958
5. Hautier, Y et al. 2015. Anthropogenic environmental changes affect ecosystem stability via biodiversity. **Science**. doi: 10.1126/science.aaa1788
6. Isbell, F et al. 2013a. Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. **PNAS**. doi: 10.1073/pnas.1310880110
7. Isbell, F et al. 2013b. Low biodiversity state persists two decades after cessation of nutrient enrichment. **Ecology Letters**. doi: 10.1111/ele.12066
8. Reich, PB et al. 2012. Impacts of biodiversity loss escalate through time as redundancy fades. **Science**. doi: 10.1126/science.1217909
9. Reich, PB et al. 2014. Plant growth enhancement by elevated CO₂ eliminated by joint water and nitrogen limitation. **Nature Geoscience**. doi: 10.1038/NGEO2284
10. Seabloom, EW et al. 2017. Food webs obscure the strength of plant diversity effects on primary productivity. **Ecology Letters**. doi: 10.1111/ele.12754

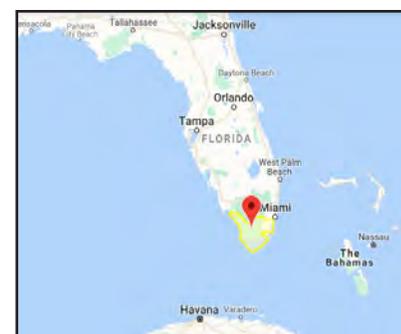


Florida Coastal Everglades LTER

Photo credit: U.S. LTER

The Florida Coastal Everglades (FCE) LTER program encompasses the subtropical freshwater wetlands, mangrove swamps, and shallow seagrass communities along the two main drainages of Everglades National Park. Fresh and marine water sources are variable in this coastal oligotrophic landscape, and interact with biogeochemical processes and human actions to modify coastal ecosystem structure, functions, and services. Since 2000, the FCE LTER program has transformed scientific understanding of the origins of coastal ecosystem productivity, particularly how nutrients regulate ecosystem response to disturbances such as tropical storms, droughts, cold snaps, shifts in freshwater management, and sea level rise.

By pairing sustained long term measurements with experiments, socio-economic studies, and modeling, the FCE LTER program fosters a mechanistic understanding of ecosystem function that influences restoration policy [Product 1]. The program is especially poised to address how the chronic stress of sea level rise affects ecosystem resilience and how disturbance legacies, social-ecological feedbacks, and regional freshwater allocation decisions may modify stress responses.



Between 2008-2018:

92 investigators

29 institutions represented

64 graduate students



Coastal

Principal Investigator:

Evelyn Gaiser

Florida International University

Est. 2000

Funding Cycle:

LTER IV

NSF Program:

Biological Sciences /
Division of Environmental
Biology



Key Findings

Hidden origins of coastal productivity.

Contradicting classical estuary models, FCE LTER research demonstrated that marine nutrient supplies (rather than freshwater nutrient supplies) control coastal productivity gradients via daily tides, episodic storm surges, and hidden groundwater upwelling. Saltwater intrusion amplifies marine pulses by increasing connectivity to the sea and liberating phosphorus from limestone. Sea level projections based on long term data were refined, painting a better picture of how water quality will be affected by shifts in freshwater supply management [2].



Disturbance interactions define coastal

gradients. Long term data reveal that multiple types of disturbances — including cold snaps, fires, droughts, floods, and tides — play a strong role in shaping coastal ecosystems. Tropical storms can be beneficial by connecting upstream and downstream food webs and dispersing mangrove propagules into disturbance-generated canopy gaps.

They also deliver phosphorus-rich mineral deposits that



promote mangrove transgression, increased soil elevation relative to sea level, and more rapid mangrove wetland recovery [4].

Sea level rise may decouple carbon sources/sinks. Rising seas can stimulate the inland transgression of mangroves and amplify carbon gains (as observed in historic carbon budgets based on long term flux data, paleoecology, and remote sensing). However, FCE LTER studies, experiments, and models show that carbon losses can exceed increases where saltwater invades freshwater marshes, resulting in abrupt elevation loss (collapse) that further promotes saltwater intrusion [3].

Donor controlled food webs. Coastal food webs are subsidized by episodic and seasonal connections to upstream detrital food supplies. However, top coastal estuary predators show great individual variation in their ability to capitalize on this subsidy — a finding that has been applied in comparative cross-site research [5].

Synthesis

Fate of massive coastal carbon stores is uncertain. Florida Coastal Everglades LTER has led and participated in comparative cross-site studies in subtropical and tropical karstic freshwater wetlands, mangrove forests, and seagrass communities — showing that carbon storage in mangrove forests far exceeds that of terrestrial woodlands [6]. The fate of these massive stores of coastal “blue carbon” will depend on how managers mitigate water quality impacts of regional land use change and how they respond to the warming, acidifying, and salinizing effects of global climate change [7]. Cross-site studies have found little connection

between the flux of organic carbon out of these systems and its availability to organisms, highlighting the importance of long term measurements to understand its fate [8].

Data Accessibility

All FCE LTER datasets collected over the past 18 years are published in the Environmental Data Initiative (EDI) repository. New and updated datasets are released to the public within two years of collection with complete metadata. Open access has led to new research and synthesis using FCE LTER datasets on flux tower, seagrass productivity, and water quality. The FCE LTER has also led international, open access LTER synthesis projects [10].

Partnerships

Everglades National Park | South Florida Water Management District | Florida International University



Broader Impacts

Long term science for society. Socio-economic, historical, and scenario studies associated with the FCE LTER contribute to understanding how decisions about Everglades restoration have been made. This has included fostering strong, lasting agency partnerships that ensure the integration of long term science into restoration policy [9].

Fostering diversity in science. Most of the undergraduate and K-12 students engaged in field and laboratory studies at FCE LTER are from the >90% majority-minority populations of Florida International University (FIU) and Miami Dade County Public Schools. Teachers are engaged in long term science, creating experiential and data-based lessons for the K-12 Schoolyard. Undergraduates serve as mentors to high school students.



Nurturing leadership. Early career scientists gain leadership experience by co-leading FCE LTER working groups. Graduate students take on leadership roles as mentors, representatives on the executive board, and participants

in Everglades Service-to-Activism workshops and congressional visits.

Science in the public sphere.

Along with 12 partner institutions, FCE

LTER promotes environmental literacy through an Artist in Residence program and four long term citizen science studies.



Photo credits: U.S. LTER (top); Steve Davis (bottom)

Top Products

1. Childers, DL et al. 2019. The Coastal Everglades: The Dynamics of Social-Ecological Transformation in the South Florida Landscape. **Oxford University Press**.
2. Dessu, SB et al. 2018. Effects of sea-level rise and freshwater management on long-term water levels and water quality in the Florida Coastal Everglades. **Journal of Environmental Management**. doi: 10.1016/j.jenvman.2018.01.025
3. Wilson, BJ et al. 2019. Phosphorus alleviation of salinity stress: effects of saltwater intrusion on an Everglades freshwater peat marsh. **Ecology**. doi: 10.1002/ecy.2672
4. Danielson, T et al. 2017. Assessment of Everglades mangrove forest resilience: Implications for above-ground net primary productivity and carbon dynamics. **Forest Ecology and Management**. doi: 10.1016/j.foreco.2017.08.009
5. Boucek, R and JS Rehage. 2014. Climate extremes drive changes in functional community structure. **Global Change Biology**. doi: 10.1111/gcb.12574
6. Rovai, A et al. 2018. Global controls on carbon storage in mangrove soils. **Nature Climate Change**. doi: 10.1038/s41558-018-0162-5
7. Fourqurean, JW et al. 2012. Seagrass ecosystems as a globally significant carbon stock. **Nature Geoscience**. doi: 10.1038/NNGEO1477
8. Jaffé, R et al. 2008. Spatial and temporal variations in DOM composition in ecosystems: The importance of long-term monitoring of optical properties. **Journal of Geophysical Research - Biogeosciences**. doi: 10.1029/2008JG000683
9. Ogden, L. 2011. *Swamplife: People, Gators and Mangroves Entangled in the Everglades*. Minneapolis: **University of Minnesota Press**.
10. Vanderbilt, K and EE Gaiser. 2017. The International Long Term Ecological Research Network: a platform for collaboration. **Ecosphere**. doi: 10.1002/ecs2.1697



Georgia Coastal Ecosystems LTER

Estuaries and marshes provide food and refuge for organisms, protect the shoreline, help keep water clean, and store carbon. The Georgia Coastal Ecosystems (GCE) LTER, based at the University of Georgia Marine Institute on Sapelo Island, was established to study long term change in coastal ecosystems. Researchers track the major drivers of long term change, such as altered freshwater input and sea level rise, and conduct experiments to assess how coastal ecosystems will respond to anticipated changes in climate and human activities. The program has made major contributions to understanding patterns of primary production, community interactions, and ecosystem services in intertidal wetlands, as well as the flow of carbon across the coastal landscape and out to the ocean. Disturbances are particularly important in the context of long term background changes such as increasing sea level. Researchers at GCE LTER will work over the coming years to systematically quantify perturbation patterns in intertidal marshes and estimate the effect of disturbance on ecosystem properties.



Between 2008-2018:

66 investigators

9 institutions represented

124 graduate students



Coastal

Principal Investigator:
Merryl Alber
University of Georgia

Est. 2000
Funding Cycle:
LTER IV

NSF Program:
Geosciences / Division of
Ocean Sciences



Key Findings

Estuaries play an outsized role in the global carbon budget. Estuaries are net sources of CO₂ to the atmosphere and coastal ocean, and net sinks for oceanic and atmospheric O₂. This finding challenges the simplistic treatment of estuaries in global carbon models, and suggests that interactions between river discharge, changes in marsh area, and increasing atmospheric CO₂ will alter shelf-ocean carbon exchange in the future. [Products 1, 2]

Ammonia oxidizers transform the nitrogen cycle. Ammonia-oxidizing archaea (AOA) convert ammonium into nitrite, but little is known about the population dynamics of this relatively new addition to the nitrogen cycle. Research from GCE LTER found that mid summer blooms of AOA coincide with a peak in nitrite concentration. Field data from 29 estuaries showed similar summer peaks in nitrite, suggesting that summer blooms of AOA are widespread and play a previously unrecognized role in driving estuarine nitrogen cycling [3].



Sea level rise alters wetland function. Sea level rise is expected to cause salt marshes to extend upstream at the expense of freshwater wetlands, dramatically altering the intertidal landscape. Experimental salinization reduces primary production, reduces plant species diversity, decreases respiration, and leads to loss of marsh elevation. [4, 5]

River flow supports marsh production. Long term monitoring, remote sensing, and field experiments showed that dominant estuarine plants grow up to 3 times better in years with low salinities, and that salinity is driven most strongly by river discharge. A high frequency of drought in 1998-2012 led to declines in plant biomass relative to the 28-year period of record for Landsat 8. [6-8]

Mobile predators structure communities. Mobile predators like alligators move between fresh and marine habitats, consume a variety of estuarine prey, and alter the behavior of intermediate predators such as blue crabs. A predator exclusion experiment initiated in 2016 indicated that blue crabs and large fish alter the abundance of marsh invertebrates such as snails and fiddler crabs, which in turn mediate plant production and soil biogeochemistry. [9]





Synthesis

Effects of shoreline armoring vary among coastal systems. Building on site specific work on coastal armoring, investigators from four coastal LTER sites developed a conceptual model of armoring and synthesized the literature, which showed that the effects of coastal armoring varied strongly and predictably among systems.

Historical analyses inform salt marsh processes. A photographic analysis of historical changes in salt marsh extent was part of an NSF Coastal SEES (Science, Engineering and Education for Sustainability) project in collaboration with two other coastal LTER sites. Topography and residential development patterns has influenced salt marsh extent over the past 70 years.

Introduced *Spartina* is changing coastal habitats in China. Introduced to China in 1979, *Spartina alterniflora* now covers almost the entire Chinese coastline. Collaborations with Chinese colleagues showed that *S. alterniflora* has far-reaching consequences for wetland processes, and that it has developed latitudinal clines in morphology and reproduction [10].

Sediment supply determines tidal marsh response to sea level rise. A collaborative NSF RUI (Research Undergraduate Institutions) project with Plum Island LTER investigated how historical and contemporary sediment delivery in east coast salt marshes regulates tidal marsh accretion in urban, agricultural, and forested landscapes.

Data Accessibility

The [GCE LTER Data Catalog](#) provides online access to datasets and is regularly synchronized to EDI and BCO-DMO data repositories, which are searchable through DataONE. Users have logged over 154,000 downloads of the site's 603 datasets. Information managers at GCE LTER have also developed several innovative software products, database systems, and web applications. The [Data Toolbox for MATLAB](#) has been downloaded by over 4,100 registered users and is actively used for sensor data harvesting and analysis at 9 other LTER sites.





Broader Impacts

Georgia Coastal Research Council (GCRC). Established in 2002, the [GCRC](#) facilitates science-based management of coastal resources for Georgia and the southeast region through workshops, scientific assessments, and synthesis of coastal research. Researchers from GCE LTER collaborate closely with the 168 scientists and managers of the GCRC.

Distributed graduate courses. A model for distributed graduate courses taught live on the internet allows GCE LTER to leverage personnel across the LTER network and beyond. This program has reached 150 students at more than 40 institutions and provides a level of expertise that no single institution could match.

Long term partnerships with educators. Students and educators in the GCE LTER Schoolyard program return year after year to be immersed in hands on research activities alongside researchers. One long time participant (Halley Page) received the prestigious Presidential Award for Excellence in Science and Mathematics Teaching.

Partnerships

National PhenoCam Network | USGS | National Atmospheric Deposition Program | Sapelo Island National Estuarine Research Reserve



Top Products

1. Cai, WJ 2011. Estuarine and Coastal Ocean Carbon Paradox: CO2 Sinks or Sites of Terrestrial Carbon Incineration? **Annual Review of Marine Science**. doi: 10.1146/annurev-marine-120709-142723
2. Wang, S et al. 2017. Inorganic carbon and oxygen dynamics in a marsh-dominated estuary. **Limnology and Oceanography**. doi: 10.1002/lno.10614
3. Hollibaugh, JT et al. 2014. Seasonal variation in the metratranscriptomes of a Thaumarchaeota population from SE USA coastal waters. **ISME Journal**. doi: 10.1038/ismej.2013.171
4. Craft, CB et al. 2009. Forecasting the effects of accelerated sea level rise on tidal marsh ecosystem services. **Frontiers in Ecology and the Environment**. doi: 10.1890/070219
5. Herbert, E et al. 2018. Differential effects of chronic and acute simulated seawater intrusion on tidal freshwater marsh carbon cycling. **Biogeochemistry**. doi: 10.1007/s10533-018-0436-z
6. Wieski, K and Pennings, SC. 2014. Climate Drivers of Spartina alterniflora Saltmarsh Production in Georgia, USA. **Ecosystems**. doi: 10.1007/s10021-013-9732-6
7. O'Donnell, J and Schalles, JF. 2016. Examination of Abiotic Drivers and Their Influence on Spartina alterniflora Biomass over a Twenty-Eight Year Period Using Landsat 5 TM Satellite Imagery of the Central Georgia Coast. Special Issue: Remote Sensing in Coastal Environments. **Remote Sensing**. doi: 10.3390/rs8060477
8. Di Iorio, D and Castelao, R. 2013. The Dynamical Response of Salinity to Freshwater Discharge and Wind Forcing in Adjacent Estuaries on the Georgia Coast. Special Issue: Coastal Long Term Ecological Research. **Oceanography**. doi: 10.5670/oceanog.2013.44
9. Nifong, JC et al. 2015. Size, sex, and individual-level behavior drive intra-population variation in cross-ecosystem foraging of a top-predator. **Journal of Animal Ecology**. doi: 10.1111/1365-2656.12306
10. Liu, W et al. 2017. Provenance-by-environment interaction of reproductive traits in the invasion of Spartina alterniflora in China. **Ecology**. doi: 10.1002/ecy.1815

Photo credits: Erika Zambello / U.S. LTER

Hubbard Brook LTER

Photo credit: Claire Nemes

The mission of Hubbard Brook (HBR) LTER is to improve understanding of the response of Northern Forest ecosystems to natural and anthropogenic disturbances. Research takes place primarily at the Hubbard Brook Experimental Forest in the White Mountains of New Hampshire. Hubbard Brook research is organized around three drivers of disturbance: 1) changing atmospheric chemistry, 2) changing climate, and 3) changing biota, which includes changes in forest structure and plant and animal species composition.

Long term measurements and experiments have led to seminal research on trends, impacts, and recovery from acid rain and other forms of atmospheric deposition, ecological impacts of forest harvesting practices, long term vegetation dynamics in forests, and songbird population trends. Future research will emphasize the interactions between current disturbances and the legacies of past disturbance.



Between 2008-2018:

36 investigators

23 institutions represented

154 graduate students



Forest

Principal Investigator:

Gary Lovett

Cary Institute of Ecosystem
Studies

Est. 1988

Funding Cycle:

LTER VI

NSF Program:

Biological Sciences /
Division of Environmental
Biology



Key Findings

Patterns of streamwater nitrogen loss from the watershed are not consistent with expectations. A mismatch between theory and data has led HBR LTER researchers to re-examine the role of denitrification, the role of mineral soil in nitrogen dynamics during succession, and the role of climate change in “tightening” the nitrogen cycle. [Products 1, 2]



Songbird populations have declined dramatically since measurements began in 1968, but show signs of stabilizing in recent years. Songbird declines are primarily due to the loss of neotropical migrant species, particularly species that nest and forage in mid-successional habitats. These species have become less common as the forest has matured [3].



Calcium is critical to forests exposed to acid rain.

De-acidification of an entire watershed through calcium silicate application led to improved tree growth, health, and reproduction; increased decomposition and loss of soil organic matter; decreased root growth; and increased loss of nitrogen in streamwater starting ~10 years after application. Lack of calcium may be inhibiting the regeneration of sugar maple in harvested watersheds. [4, 5]

Climate change affects forest productivity. Climate change has extended the growing season and altered conditions during seasonal transitions. It has also had significant effects on the fluxes of whole-system carbon and nitrogen. [6, 7]

Partnerships

U.S. Forest Service | Hubbard Brook Research Foundation (HBRF) | National Atmospheric Deposition Program (NADP) (member) | U.S. EPA Clean Air Status & Trends Network (CASTnet) (member) | DroughtNet (member)





Synthesis

Quantifying uncertainty in ecosystem studies.

Researchers at HBR LTER have led LTER-wide collaborations to characterize and share sources of uncertainty related to data on soils, biomass, atmospheric deposition, stream water export, and ecosystem budgets. Overall, the goal was to improve data quality and usefulness for modeling.



Photo credits: Jane Sokolow (top); HBR LTER (above); Scott Schwenk (right)

Forest pests. Hubbard Brook, Harvard Forest LTER, and others summarized existing knowledge on the ecological and economic impacts of imported forest pests in the U.S., and evaluated policy options for reducing future importation of new pests.



Soil methane uptake.

Joint studies from HBR LTER, Baltimore Ecosystem Study LTER, and other international sites demonstrated decreased soil methane uptake over time. This finding may help explain why atmospheric levels of this potent greenhouse gas have been increasing globally [8].

Data Accessibility

Hubbard Brook hydrologic records began in 1955, watershed chemical inputs and outputs began in 1963, and continuous songbird population recording began in 1968. The information management system at HBR LTER maintains an accessible catalog of Hubbard Brook data with an emphasis on high quality and maintains a physical sample archive.

The HBR Information Manager established a workflow from field/lab data collections to the Environmental Data Initiative (EDI) data repository, where data are open access. The majority of the 1,000 annual downloads come from outside the HBR LTER. These data also support K-12 curricula and synthesis activities between LTER sites and beyond.

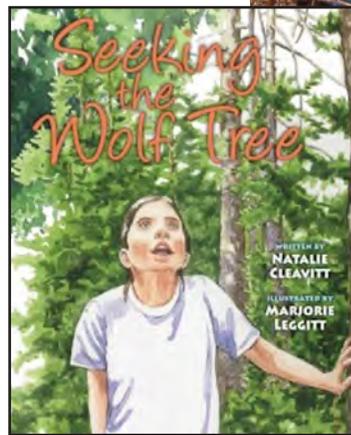
Broader Impacts

Hubbard Brook Roundtables connect HBR LTER scientists with decision-makers.

Roundtables at HBR LTER are facilitated dialogues between scientists and decision-makers. Topics have included climate change impacts on forests, the maple industry, snowmobiling, wood fuel, public engagement with science, forests in a climate economy, biodiversity, and preventing forest pest importation.

Engaging teachers and the next generation of ecosystem thinkers.

Each year approximately 6,000 students and teachers participate in HBR LTER education programs, which include K-12 classroom resources, guided and virtual tours of the Hubbard Brook Experimental Forest, and continued education for teachers, such as training workshops and summer field research experience. In addition, the HBR Research Experience for Undergraduates (REU) offers hands on science training for up to ten undergraduate students per summer.



Linking scientific information with public policy.

Hubbard Brook Research Foundation established the “Science Links” series of reports and is a founding member of the Science Policy Exchange, a consortium dedicated to the sound use of science in federal policy. Products include a fact sheet about climate change, a summary for community leaders on reducing carbon emissions, synthesis and outreach on the health and environmental co-benefits of reducing carbon dioxide emissions, and the ecological and economic impacts of invasive forest pests.

Photo credit: Kevin McGuire (top)

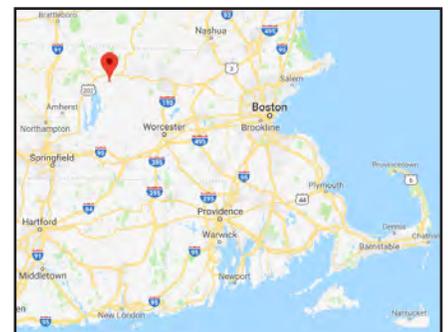
Top Products

1. Yanai, RD et al. 2013. From missing source to missing sink: Long-term changes in the nitrogen budget of a northern hardwood forest. **Environmental Science & Technology**. doi: 10.1021/es4025723
2. Lovett, GM et al. 2018. Nutrient retention during ecosystem succession: a revised conceptual model. **Frontiers in Ecology and the Environment**. doi: 10.1002/fee.1949
3. Holmes, RT. 2011. Avian population and community processes in forest ecosystems: Long-term research in the Hubbard Brook Experimental Forest. **Forest Ecology & Management**. doi: 10.1016/j.foreco.2010.06.021
4. Battles, JJ et al. 2014. Restoring soil calcium reverses forest decline. **Environmental Science & Technology Letters**. doi: 10.1021/ez400033d
5. Rosi-Marshall, EJ et al. 2016. Acid rain mitigation experiment shifts a forested watershed from a net sink to a net source of nitrogen. **PNAS**. doi: 10.1073/pnas.1607287113
6. Groffman, PM et al. 2012. Long-term integrated studies show complex and surprising effects of climate change in the northern hardwood forest. **BioScience**. doi: 10.1525/bio.2012.62.12.7
7. Keenan, TF et al. 2014. Net carbon uptake has increased through warming-induced changes in temperate forest phenology. **Nature Climate Change**. doi: 10.1038/NCLIMATE2253
8. Ni, X and PM Groffman. 2018. Declines in methane uptake in forest soils. **PNAS**. doi: 10.1073/pnas.1807377115
9. Campbell, JL et al. 2011. Streamflow responses to past and projected future changes in climate at the Hubbard Brook Experimental Forest, New Hampshire, United States. **Water Resources Research**. doi: 10.1029/2010wr009438
10. McGuire, KJ et al. 2014. Network analysis reveals multiscale controls on streamwater chemistry. **PNAS**. doi: 10.1073/pnas.1404820111



Harvard Forest LTER

The Harvard Forest (HFR) LTER program is based at the Harvard Forest, Harvard University's 2,000 ha outdoor classroom and laboratory in central Massachusetts. Harvard Forest research is dedicated to understanding how New England's temperate forests function and are affected by natural and human forces. In its first 30 years, the program has transformed scientific understanding of how forest ecosystems respond to disturbances, such as land use and hurricanes, and to chronic stressors, such as air pollution and climate change. The program has demonstrated the persistent ecological legacies of past conditions and their central role in shaping future forests. Through the combination of deep historical studies, sustained measurements and experiments, and modeling, HFR LTER has developed a mechanistic understanding of ecosystem function and is poised to predict the impacts of global change on temperate forest ecosystems from site to regional scales.



Between 2008-2018:

43 investigators

15 institutions represented

51 graduate students



Forest

Principal Investigator:
Jonathan Thompson
Harvard University

Est. 1988
Funding Cycle:
LTER VI

NSF Program:
Biological Sciences /
Division of Environmental
Biology



Key Findings

Carbon uptake exceeds expectations.

Contradictory to theoretical models, forest carbon uptake has accelerated over recent decades in maturing forests, a legacy of 19th century land use, and to a lesser degree, modern increases in atmospheric CO₂, nitrogen deposition, temperature, and precipitation. This and many other insights into forest ecosystem function have resulted from sustained measurements of biosphere-atmosphere exchanges at HFR's Environmental Monitoring Site (EMS) eddy flux tower, which provides the world's longest record of CO₂ fluxes in a forest ecosystem. It is also the founding prototype for the AmeriFlux network and National Ecological Observation Network (NEON). [Products 1-3]

Microbes respond to global change. Decades of experimental soil warming and nitrogen enrichment have induced adaptive responses in microbial communities, abruptly shifting soil carbon dynamics. The experiments have revealed phased responses to warming, oscillating between multi year periods of significant soil carbon loss and phases of no carbon loss. [4,5]

Hemlock is a foundation species. Three decades of research on abrupt declines in pre-European hemlock populations, long term regional measurements of hemlock decline from the invasive insect hemlock woolly adelgid, and the long term Hemlock Removal Experiment confirm that hemlocks are a foundation species.

They control forest structure, composition, and microclimate, with cascading trophic effects extending from mammals to microbes. As invasive insects proliferate across North America, HFR LTER is developing a generalizable understanding of population, community, and ecosystem level responses. [6,7]

Spring is arriving earlier. Over the last 30 years, spring phenology has advanced across eastern North America, increasing photosynthesis and net ecosystem carbon storage, with a small negative feedback to climate change. Beginning in 1990 as a biannual pen-and-paper record of bud break and leaf fall, HFR LTER launched the PhenoCam Network in 2008, a continental scale observatory of digital imagery tracking phenology at fine spatial and temporal scales [8].





Synthesis

Science for society takes a village. As a founder of the Science Policy Exchange, HFR LTER often co-designs studies with public and private partners to use long term data to solve real world problems. Products range from policy and management recommendations for rare species management, land protection goals, and responses to natural and human disturbances to simulations of land use and climate change scenarios that quantify consequences for critical ecosystem services and help guide land planning and conservation. [9, 10]

Partnerships

NEON | AmeriFlux |
Smithsonian/ForestGEO
| PhenoCam Network |
Harvard University



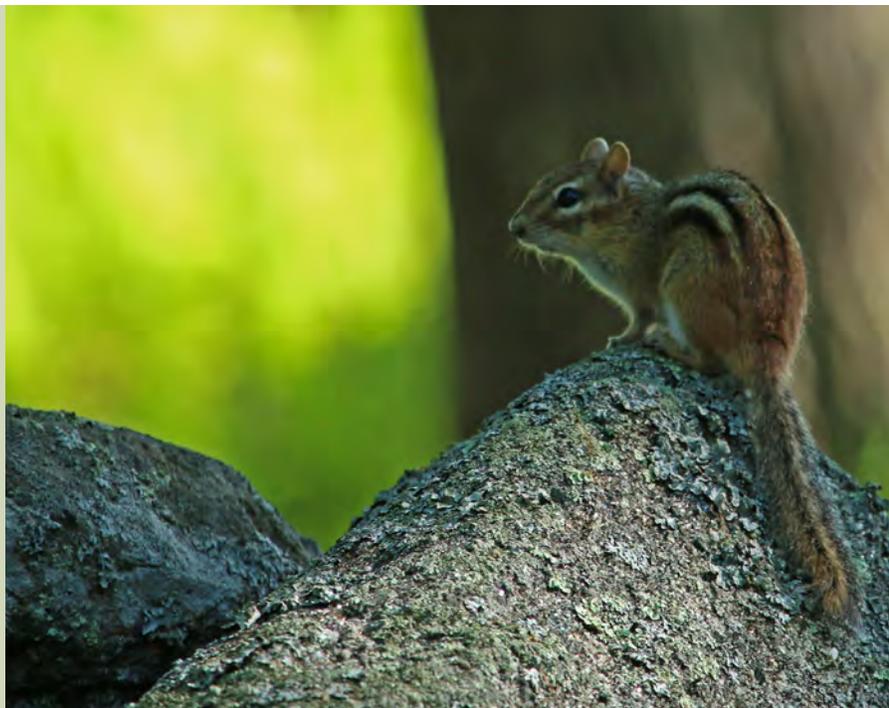
AMERIFLUX



National Ecological Observatory Network

Data Accessibility

The Harvard Forest data archive contains data collected over the last 30 years from all studies at or pertaining to Harvard Forest, regardless of the source of funding, as well as selected data, photography, and cartography since 1907 from the Harvard Forest Archives. New datasets and updates are posted simultaneously to the Harvard Forest (HF) data archive (where they are cross indexed with the online HF bibliography) and to the Environmental Data Initiative (EDI) repository.



Broader Impacts

Wildlands, Woodlands, Farmlands and Communities. With the Highstead Foundation and many public and private partners, HFR LTER is advancing a regional conservation effort by providing science based tools and training for more than 300 partner agencies and organizations in New England.

Local, long term classroom data. The Schoolyard Ecology Program leverages LTER funding by a factor of four and engages more than 50 teachers and 3,700 students annually in a science literacy program rooted in field data collection. Investigators at HFR LTER lead workshops to help classrooms explore, compare, and graph their field data using an online system designed by the HFR Information Manager. More than 240 classrooms have submitted data and several datasets now span more than a decade. All teacher created lesson plans, plus a “data nugget” exploring a signature HFR dataset, are publicly available online.



Team science for diverse undergrads.

Harvard Forest’s world class summer research program draws 20-30 Research Experience for Undergraduates (REU) students annually (>40% from traditionally underrepresented groups) to work on mentored, team based projects. Assessment shows that most program alumni go on to study or work in environmental fields and that benefits are greatest for students from traditionally underrepresented groups and those who lack prior research experience.

Landscape Scenarios.

Stakeholders from every New England state contribute to and use results and tools from LTER based landscape scenarios research, which examines ecological

consequences of alternative scenarios of climate and land use change.

LTER based partnerships. Collaborations with artists, writers, and designers through leveraged funding has resulted in many books, exhibits, public events, and conference and classroom presentations.

Top Products

1. Finzi, AC et al. 2019. The Harvard Forest carbon budget: patterns, processes and responses to global change. **Ecological Monographs**. (in review)
2. Wehr, R et al. 2016. Seasonality of temperate forest photosynthesis and daytime respiration. **Nature**. doi: 10.1038/nature17966
3. Urbanski, SP et al. 2007. Factors controlling CO2 exchange on time scales from hourly to decadal at the Harvard Forest. **Journal of Geophysical Research - Biogeosciences**. doi: 10.1029/2006JG000293
4. Melillo, JM et al. 2017. Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. **Science**. doi: 10.1126/science.aan2874
5. Frey, SD et al. 2013. The temperature response of soil microbial efficiency and its feedback to climate. **Nature Climate Change**. doi: 10.1038/NCLIMATE1796
6. Foster, DR et al. 2014. Hemlock: A Forest Giant on the Edge. **Yale University Press**.
7. Ellison, AM et al. 2010. Experimentally testing the role of foundation species in forests: The Harvard Forest Hemlock Removal Experiment. **Methods in Ecology and Evolution**. doi: 10.1111/j.2041-210X.2010.00025.x
8. Keenan, TF et al. 2014. Net carbon uptake has increased through warming-induced changes in temperate forest phenology. **Nature Climate Change**. doi: 10.1038/NCLIMATE2253
9. Lovett, GM et al. 2016. Nonnative forest insects and pathogens in the United States: Impacts and policy options. **Ecological Applications**. doi: 10.1890/15-1176
10. Thompson, JR et al. 2014. Changes to the Land: Four Scenarios for the Future of the Massachusetts Landscape. Harvard Forest, **Harvard University**.



Jornada Basin LTER

The goal of the Jornada Basin (JRN) LTER program is to understand and quantify the key factors and processes controlling ecosystem dynamics and state changes in Chihuahuan Desert landscapes. Studies beginning in 1915 have been incorporated into the JRN LTER in collaboration with the Jornada Experimental Range (USDA Agricultural Research Service, Las Cruces, NM). Short and long term field studies, multi-scale pattern analyses, simulations, and experimental manipulations are used to challenge the typical assumption that shifts from grassland to shrubland in desert landscapes is always inevitable and irreversible.

Instead, trigger events, such as grazing or precipitation, interact with wind, water, and other resources to affect ecosystem dynamics at multiple spatial and temporal scales. Work from JRN LTER is informing a comprehensive framework that can be applied to other drylands around the world.



Between 2008-2018:

14 investigators

10 institutions represented

72 graduate students



Grassland

Principal Investigator:

Debra Peters

New Mexico State University

Est. 1982

Funding Cycle:

LTER VII

NSF Program:

Biological Sciences /
Division of Environmental
Biology



Key Findings

Insights into vegetation change. The shift from grassland to shrubland is not the only alternative state for desert vegetation. Jornada Basin LTER research has documented shifts from desertified shrublands back towards native grassland, and shifts from grass or shrublands to novel ecosystems dominated by non-native annual or perennial grasses. State changes depend on wind and water movement patterns, spatial variation in soil and vegetation type, and triggers such as multiple years of precipitation and livestock grazing at levels above or below average precipitation.

[Products 1-4]

Connectivity plays a key role in vegetation dynamics. Locations that are functionally connected in the landscape experience greater materials and energy transfer, which ultimately influences spatial and temporal vegetation dynamics in desert landscapes.

In pilot studies, small connectivity modifying structures (ConMods)

increased

grasses and forbs



relative to areas without ConMods [5].

Sources of groundwater recharge. Using long term observations and a water balance approach, JRN LTER researchers determined that small watersheds on piedmont slopes are large contributors to groundwater recharge on the Jornada Basin. This was one of the first studies to quantify groundwater recharge in arid region first-order watersheds [6].

Rodent biomass linked to precipitation. Desert rodent biomass depends on an interaction between shrub cover and precipitation – more rodent biomass is associated with grasslands following droughts and with shrublands following wet years. This pattern can be largely explained by the irruption of folivores (which prefer shrubbier vegetation) during wet years and suggests that rodent population dynamics are likely to change following climatic shifts [7].

The power of “Big Data.” Researchers at JRN LTER are incorporating machine learning into complex dataset exploration. The data exploration interface is capable of suggesting potential analytical approaches to new users based on interactions with previous users [8].



Synthesis

Co-founder of the EcoTrends Project. Jornada Basin LTER researchers developed and maintain a long term archive of data and products from many long term monitoring sites on the EcoTrends website. [EcoTrends](#) is particularly valuable for increasing data accessibility to high school students, journalists, and citizen scientists.

Leading desert research. Jornada Basin LTER funded and contributed to several special issues: *Frontiers in Ecology and the Environment* (“Emerging perspectives and shifting paradigms in water-limited systems”, 2015), *BioScience* (“Connectivity and scale in dryland ecosystems”, 2018), and *Ecosphere* (Dynamic Deserts, to be published 2019).

Partnerships

USDA Agricultural Research Service
Jornada Experimental Range program |
New Mexico State University



Data Accessibility

The Jornada Basin LTER data collected over the last 30+ years is stored in a data archive and posted to the Environmental Data Initiative Repository (EDI). Researchers at JRN LTER are currently developing tools that will enhance collaboration, including sharing data in real-time from meteorological stations and using RStudio to visualize and present key datasets.



Broader Impacts

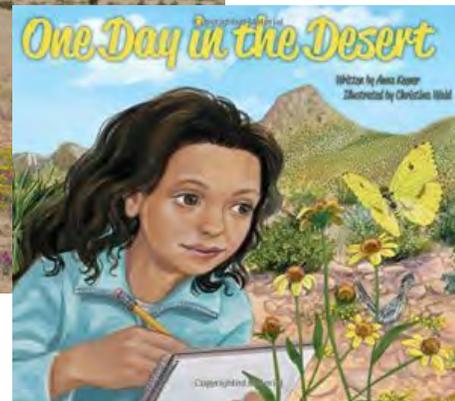
Supporting diverse participation. Jornada Basin LTER supports graduate and undergraduate students from a diverse set of institutions and disciplines, and attracts postdocs and visiting scientists from around the world. New Mexico

State University, University of Texas, El Paso, Arizona State University, and University of Arizona are frequent collaborators that are also minority, Hispanic serving institutions.

The Jornada Basin LTER K-12 education program primarily engages underserved students – 84% of participants are economically disadvantaged and 82% are Hispanic.



for more than 15,000 students each year. In addition, the JRN Schoolyard LTER program develops and broadly disseminates models of K-12 science education. The Jornada middle school Data Jam competition engages up to 500 students per year and is now being replicated at other LTER sites [9].



Developing innovative K-12 education.

In collaboration with Asombro Institute for Science Education, the Jornada Basin Schoolyard LTER program includes field trips, classroom/schoolyard lessons, and teacher workshops to improve K-12 science literacy

Informing land management. Jornada LTER scientists spearheaded the development of rangeland monitoring protocols that have been adopted by the Natural Resources Conservation Service and the Bureau of Land Management. The LandPKS app estimates soil and vegetation properties in the field [10].

Top Products

1. Peters, DPC, et al. 2014. Mechanisms of grass response in grasslands and shrublands during dry or wet periods. **Oecologia**. doi: 10.1007/s00442-013-2837-y
2. Peters, DPC, et al. 2015. Beyond desertification: new paradigms for dryland landscapes. **Frontiers in Ecology and the Environment**. doi: 10.1890/140276
3. Bestelmeyer, BT, et al. 2013. A test of critical thresholds and their indicators in a desertification-prone ecosystem: more resilience than we thought. **Ecology Letters**. doi: 10.1111/ele.12045
4. Sala, OE, et al. 2012. Legacies of precipitation fluctuations on primary production: theory and data synthesis. **Philosophical Transactions of the Royal Society B**. doi: 10.1098/rstb.2011.0347
5. Okin, GS, et al. 2015. Connectivity in dryland landscapes: shifting concepts of spatial interactions. **Frontiers in Ecology and the Environment**. doi: 10.1890/140163
6. Schreiner-McGraw, AP and Vivoni ER. 2017. Percolation observations in an arid piedmont watershed and linkages to historical conditions in the Chihuahuan Desert. **Ecosphere**. doi: 10.1002/ecs2.2000
7. Schooley, RL, et al. 2018. Shrub encroachment, productivity pulses, and core-transient dynamics of Chihuahuan Desert rodents. **Ecosphere**. doi: 10.1002/ecs2.2330
8. Peters, DPC, et al. 2014. Harnessing the power of big data: infusing the scientific method with machine learning to transform ecology. **Ecosphere**. doi: 10.1890/ES13-00359.1
9. Bestelmeyer, SV, et al. 2015. Collaboration, interdisciplinary thinking, and communication: new approaches to K-12 ecology education. **Frontiers in Ecology and the Environment**. doi: 10.1890/140130
10. Herrick, JE, et al. 2013. The global land-potential knowledge system (LandPKS): Supporting evidence-based, site-specific land use and management through cloud computing, mobile applications, and crowdsourcing. **Journal of Soil and Water Conservation**. doi: 10.1002/ehs2.1209



Kellogg Biological Station LTER

Photo credit: Kevin Kahmark / KBS LTER

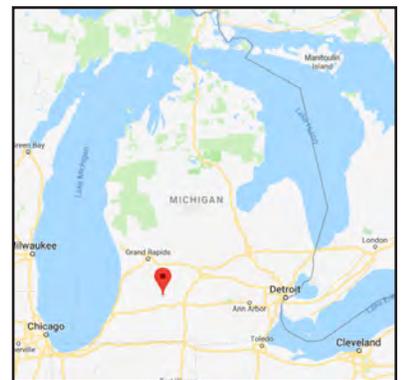
Since 1988, Kellogg Biological Station (KBS) LTER has been the only LTER site focusing on agricultural cropping systems, which occupy 1.5 million ha in the United States. Research from KBS LTER has advanced understanding of how agronomic management based on ecological knowledge can better deliver ecosystem services, including yield, greenhouse gas mitigation, nutrient conservation, and pest suppression. Socio-ecological research at KBS LTER reveals how farmers perceive and provide ecosystem services. By simultaneously considering both natural and human factors across a mosaic of agricultural and non-agricultural land covers, KBS LTER research reveals mechanisms that contribute to the resilience of important populations and processes in agricultural landscapes in the face of increasing pressures from long term land use and climate change.

Between 2008-2018:

235 investigators

37 institutions represented

204 graduate students



Mixed Landscape

Principal Investigator:
Nick Haddad
Michigan State University

Est. 1988
Funding Cycle:
LTER VI

NSF Program:
Biological Sciences /
Division of Environmental
Biology



Key Findings

Environmental management can mitigate greenhouse gas emissions. Agriculture emits quantities of greenhouse gases equivalent to those from the transportation sector, and long term LTER research has revealed how farmers can better manage intensive row crop systems to mitigate climate change. Plant-microbe-soil interactions can enhance soil carbon sequestration, reduce nitrous oxide emissions, and promote methane oxidation. Implemented widely, improved management could make cropping systems a major mitigator of climate change. [Products 1-4, 7, 8, 10]

Landscape diversity enhances pest suppression. Simplification of agricultural landscapes reduces abundance of predatory insects, at substantial cost to farmers and society. Diverse landscapes harbor generalist predators such as ladybird beetles, which control crop pests such as soybean aphids, limiting the need for insecticide use. Given global declines in insect abundance, increasing the diversity of habitats and their spatial

arrangement across landscapes could enhance biodiversity and provide biocontrol services worth hundreds of millions of dollars per year, while reducing the need for insecticides. [3, 10]

Evolutionary responses of microbes that underpin functions and services. Twenty-plus years of nitrogen fertilization have caused rhizobia in soybeans to evolve toward reduced nitrogen fixation. These evolutionary changes have ecological consequences, as the evolution of reduced cooperation alters soil nitrogen availability. Directed changes to the microbial community, through plant-soil management or added bioinoculants, represents an important frontier for improving cropping system resilience. [3, 9]

Consumers express willingness to pay for ecosystem services from agriculture. Research from KBS LTER reveals not only how changes in cropping practices improve ecosystem service flows, but also the economic value of those flows. Paired studies of farmers and consumers track farmer willingness to provide changed practices along with consumer willingness to pay for ecosystem services that come from those changed practices, such as climate mitigation, water quality regulation, and natural pest control. [3, 5]





Synthesis

The Lotic Intersite Nitrogen Experiment (LINX) was a 17-year cross-site collaboration among scores of stream ecologists to better understand how streams process watershed nitrogen inputs. Researchers at KBS LTER played a pivotal role in methods development and lab analyses. In partnership with Andrews Experimental Forest LTER, KBS LTER built an accessible online database of all LINX data.

The “Productivity-Diversity” project began in 1996 when 16 LTER sites convened with the goal of examining the relationship between Annual

Net Primary Productivity (ANPP) and species diversity. Eleven sites with herb-dominated plant communities (including KBS LTER) joined in a now 20+ year synthesis as the Productivity-Diversity-Traits Network (PDTNet) to better understand ANPP and its environmental drivers.

Partnerships

Department of Energy Great Lakes Bioenergy Research Center | U.S. Department of Agriculture Long-Term Agroecosystem Research (LTAR) | AmeriFlux | National Phenology Network | Nutrient Network (NutNet) | Aerosol Robotic Network

Data Accessibility

Kellogg Biological Station LTER maintains an online catalog of data collected at the site. Snapshots are periodically submitted to the Environmental Data Initiative (EDI) repository. The catalog also includes a spatial data and aerial image repository dating back to the 1960s.

Photo credits: Kurt Stepnitz Photography



Broader Impacts

Getting data into classrooms. The KBS LTER K-12 partnership between LTER researchers and rural school districts has been supported by Schoolyard LTER funds and two NSF Graduate STEM Fellows in K-12 Education (GK-12) awards at KBS LTER. The partnership developed Data Nuggets to bring ecological science into Kindergarten through college classrooms. These curricula use LTER data contributed by KBS LTER and other sites, and are used by teachers in all 50 states and in 140 countries.

Connecting with the real world. Research at KBS LTER bears directly on agricultural management and policies at local (e.g., soil and water conservation) to global scales (climate change mitigation). LTER researchers conduct surveys and discussion forums for scientists, farmers, extension educators, government and state agency staff, industry, and private sector farm advisors to build the foundation for making their research more translational to — and informed by — diverse stakeholders. Strengthening public-private networks and collaborations



Photo credit: Kurt Stepnitz Photography

Mentoring the next generation.

Undergraduate research interns, many from underrepresented groups, are a highlight of the KBS LTER program. Through their blog posts, they describe the transformative and educational values of time at KBS. Carlnesia Johnson, an REU student in 2017, wrote:

“I have never worked so hard for anything in my life until I came to KBS. I was forced to gain confidence because it would've been a hard summer without it. I didn't come into my newly found confidence alone though; it was because of my mentor, my lab family, peers, and other people at KBS.”

is imperative to effecting change in agricultural management.

Informing greenhouse gas policies. Partnering with agricultural professionals and industry, KBS LTER developed a carbon credit protocol for agricultural nitrogen management to allow farmers to participate in voluntary carbon credit markets. This protocol, the first for nitrogen, compensates farmers for precise application of nitrogen fertilizer in order to reduce nitrous oxide emissions.

Top Products

1. Culman, SW et al. 2012. Permanganate oxidizable carbon reflects a processed soil fraction that is sensitive to management. **Soil Science Society America Journal**. doi: 10.2136/sssaj2011.0286
2. Gelfand, I et al. 2013. Sustainable bioenergy production from marginal lands in the US Midwest. **Nature**. doi: 10.1038/nature11811
3. Hamilton, S et al. 2015. The Ecology of Agricultural Landscapes: Long-Term Research on the Path to Sustainability. **Oxford University Press**.
4. Kravchenko, AN et al. 2017. Field-scale experiments reveal persistent yield gaps in low-input and organic cropping systems. **PNAS**. doi: 10.1073/pnas.1612311114
5. Ma, S et al. 2012. Farmers' willingness to participate in payment-for-environmental-services programs. **Journal of Agricultural Economics**. doi: 10.1111/j.1477-9552.2012.00358.x
6. Mulholland, PJ et al. 2008. Stream denitrification across biomes and its response to anthropogenic nitrate loading. **Nature**. doi: 10.1038/nature06686
7. Robertson, GP et al. 2014. Farming for ecosystem services: an ecological approach to production agriculture. **BioScience**. doi: 10.1093/biosci/biu037
8. Tiemann, LK et al. 2015. Crop rotational diversity enhances below-ground communities and functions in an agroecosystem. **Ecology Letters**. doi: 10.1111/ele.12453
9. Weese, DJ et al. 2015. Long-term nitrogen addition causes the evolution of less-cooperative mutualists. **Evolution**. doi: 10.1111/evo.12594
10. Werling, BP et al. 2014. Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. **PNAS**. doi: 10.1073/pnas.1309492111



Konza Prairie LTER

Photo credit: Jill Haukos

Konza Prairie (KNZ) LTER is focused on North American tallgrass prairie, specifically the Flint Hills ecoregion of northeast Kansas, which includes the largest tracts of unplowed tallgrass prairie in North America. Core KNZ LTER research has been based on a unique watershed-level fire and grazing experiment at the Konza Prairie Biological Station (KPBS) that began in 1972. Since then, complementary long term plot-level and stream reach experiments, and a network of sensors and sampling stations in both terrestrial and aquatic habitats have served as a foundation for the program.

Nearly four decades of KNZ LTER research has produced a rich, detailed, and evolving understanding of how fire, grazing, and climate interact to shape the structure and function of mesic grasslands. This has provided researchers with a unique opportunity to identify key drivers and mechanisms underlying ecosystem state change. Variations in fire frequency, grazing intensity, grassland restoration, nutrient input, and climate regimes have resulted in divergent ecosystem states with non-linear dynamics and strong legacy effects. By evaluating long term responses to these drivers, *(continued)*



Between 2008-2018:

66 investigators

11 institutions represented

72 graduate students



Mixed Landscape

Principal Investigator:

Jesse Nippert

Konza Prairie Biological
Station

Est. 1980

Funding Cycle:

LTER VII

NSF Program:

Biological Sciences /
Division of Environmental
Biology



KNZ LTER researchers have identified thresholds, warning signs that precede state shifts, legacies, and hysteresis. These discoveries have deepened the body of knowledge on grassland dynamics, and KNZ LTER's experimental framework is being used to test and advance theories on non-equilibrium, community assembly, meta-population, resource limitation, and ecosystems.



Key Findings



A landscape that requires disturbance. Konza Prairie Biological Station features a replicated watershed-scale experiment with contrasting fire frequency and grazing treatments.

Fire frequency affects plant composition and ecosystem state (i.e. whether

an ecosystem is grassland, shrubland, or woodland). Fire also affects nutritional quality and quantity of vegetation, which influences foraging decisions by large herbivores at multiple scales. Herbivore choices cascade to impact grassland biodiversity via changes in dominance, a mechanism which KNZ LTER researchers found to be consistent with grasslands worldwide. [Products 1-3]

Variable resistance, but high resilience of tallgrass prairie to climate change. Climate change forecasts for mesic grasslands include increased climate variability and extremes. Experimental climate manipulations at Konza Prairie reveal a spectrum of responses to climate change, ranging from a lack of resistance to extreme drought, to great

resilience to increased precipitation and heat wave variability. Although community composition changes with climate extremes, tallgrass prairie resilience is promoted by compensatory responses by dominant plant species. [4, 5]

Non-equilibrium dynamics are nearly ubiquitous and spatially complex. Experiments at KNZ LTER have identified significant time lags between treatment initiation and sustained community effects. At a minimum, these times lags are 3-6 years for water and nutrient manipulations, but can be decades according to fire suppression and woody plant expansion studies. Decreases in plant diversity evident in the first few years after water and nutrient enrichment did not necessarily persist long term due to stochastic influences on community assembly. In streams, communities reassembled and ecosystem processes recovered over weeks to months following flood or drought. These observations represent a paradigm shift in understanding grassland assembly and spatial and temporal responses to changing external drivers. [6-8]





Photo credit: Eva Horne

Synthesis

ILTER cross-site synthesis working groups.

Investigators from KNZ LTER have shared data and participated in several LTER synthesis working groups (2016-present) including: Ecosystem Sensitivity to Rainfall Experiment (EcoSeRE): design and synthesis, Long term experiments in the LTER Network: synthesis and hypothesis testing, and Integrating Plant Community and Ecosystem Responses to Chronic Global Change Drivers: Toward an Explanation of Patterns and Improved Global Predictions, which includes data from 7 LTER sites [9].

Framework for Stream Ecology. The stream biome gradient framework was created by KNZ LTER scientists to globally contextualize streams using surrounding terrestrial biomes to predict aspects of stream ecology (e.g. ecophysiology and ecosystems). Cross-site syntheses investigate nitrogen dynamics in food webs, leaf decomposition rates in response to climate change, and top-down control of stream consumers on stream ecosystem processes [10].



Photo credit: Jesse Nippert

Data Accessibility

The Information Management System (IMS) at KNZ LTER includes over 1,800 publications and 295 related datasets from 129 projects. All are available via the KNZ LTER website (using an interactive search interface), the Environmental Data Initiative Data Portal, and DataONE.

Partnerships

Konza Prairie Biological Station | The Nature Conservancy | Kansas State University | NEON Core Site | founding member of Nutrient Network (NutNet) | founding member of DroughtNet | Ameriflux Site



Broader Impacts

Connecting science to K-12 education. The Konza Schoolyard LTER program engages local teachers and 800-1,000 students per year. Participants use KNZ LTER data, collect their own during site visits, and share findings in collaborative learning and research activities. The broader Konza Environmental Education Program (KEEP) facilitates science education and activities at KPBS for 2,500-3,000 schoolchildren annually.



Linking science and art. Konza Prairie LTER and KPBS collaborate with the local Prairie Studies Initiative, run by Kansas State University faculty, staff, students, and the public. The Initiative explores cultural and ecological dimensions of the prairie and challenges to sustaining grassland. This program connects scientists to poets, essayists, photographers, painters, and artists.

Conservation and stewardship. Scientists at KNZ LTER and KPBS have led tours for 3,000+ individuals associated with over 50 grassland-related professional groups. They have also worked closely with The Nature Conservancy to connect grassland science to best restoration and conservation practices. In 2017, KPBS hosted over 80 grassland practitioners at the annual Grassland Restoration Network workshop.

Top Products

1. Raynor EJ, et al. 2015. Bison foraging responds to fire frequency in nutritionally heterogeneous grassland. **Ecology**. doi: 10.1890/14-2027.1
2. Koerner SE, et al. 2018. Changes in dominance determine herbivore effects on plant biodiversity. **Nature Ecology and Evolution**. doi: 10.1038/s41559-018-0696-y
3. Welti EAR, et al. 2019. Fire, grazing, and climate shape plant-grasshopper interactions in a tallgrass prairie. **Functional Ecology**. doi: 10.1111/1365-2435.13272
4. Hoover DL, et al. 2014. Resistance and resilience of a grassland ecosystem to climate extremes. **Ecology**. doi: 10.1890/13-2186.1
5. Knapp AK, et al. 2018. A reality check for climate change experiments: Do they reflect the real world? **Ecology**. doi: 10.1002/ecy.2474
6. Ratajczak Z, et al. 2014. Fire dynamics distinguish grasslands, shrublands, and woodlands as alternative attractors in the Central Great Plains of North America. **Journal of Ecology**. doi: 10.1111/1365-2745.12311
7. Avolio ML, et al. 2014. Changes in plant community composition, not diversity, during a decade of nitrogen and phosphorus additions drive above-ground productivity in a tallgrass prairie. **Journal of Ecology**. doi: 10.1111/1365-2745.12312
8. Baer SG, et al. 2016. Environmental heterogeneity has a weak effect on diversity during community assembly in tallgrass prairie. **Ecological Monographs**. doi: 10.1890/15-0888.1
9. Wilcox KR, et al. 2017. Asynchrony among local communities stabilises ecosystem function of metacommunities. **Ecology Letters**. doi: 10.1111/ele.12861
10. Dodds WK et al. 2015. The Stream Biome Gradient Concept: Factors controlling lotic systems across broad biogeographic scales. **Freshwater Science**. doi: 10.1002/ecs2.2786

Photo credit: Jaime Schirmer (top)

Photo credits (page 2): Barbara Van Slyke (top, bottom); Eva Horne (middle)



Luquillo LTER

Luquillo (LUQ) LTER is located in the Luquillo Mountains of eastern Puerto Rico, home to the 11,330 hectare Luquillo Experimental Forest. Also known as the El Yunque National Forest, it is the oldest forest preserve in the Western Hemisphere. Struck by three major hurricanes within 30 years, LUQ LTER has transformed current understanding of how tropical forests respond to altered disturbance regimes and highlighted the importance of antecedent events in determining those dynamics. Regional droughts and a warming experiment at LUQ LTER are case studies for the likely impacts of predicted climate change at the end of the century. Work at LUQ LTER illuminates the intricate web of interactions between climate, disturbance, biogeochemistry, and ecological communities, and provides an important laboratory for quantifying the impacts of climate change on tropical forest ecosystems.



Between 2008-2018:

- 39** investigators
- 19** institutions represented
- 37** graduate students



Forest

Principal Investigator:
 Jess K. Zimmerman
 University of Puerto Rico

Est. 1998
 Funding Cycle:
 LTER VI

NSF Program:
 Biological Sciences/
 Division of Environmental
 Biology



Key Findings

Hurricane frequency impacts forest biodiversity and ecosystem function. The long term Canopy Trimming Experiment revealed many important aspects of hurricane disturbance, particularly that canopy opening caused more change in biota and biogeochemistry than debris deposition. More frequent disturbance led to canopy opening but less debris deposition, and changed forest species composition, which

may alter resilience in the face of future disturbances. Frequent hurricane disturbance causes forest ecosystems to retain less carbon and export more nutrients. [Products 1, 4, 6-9]



Drought in rainforests is increasing in a warming world. Drought in tropical wet forest alters greenhouse gas production by soils, affects key nutrient

dynamics, and reduces forest productivity.

Downscaling studies at LUQ LTER support global models that predict declining precipitation through the end of the century. Current ecosystem drying and warming model projections predict that net forest ecosystem productivity may fall to zero by 2036. A long term streamflow reduction experiment will determine impacts of long term drought on stream functioning. [2, 10]

Climate change will impact lower elevation forests first. Luquillo LTER uses an elevation gradient as a proxy for studying certain aspects of climate change. High elevation cloud forests on mountain summits harbor many endemic species likely to be threatened by the changes in precipitation and temperature projected to impact these areas within 20 years. Recording changes in biota and critical ecosystem function along the elevational gradient through the year 2100 will capture key aspects of the changing climate and disturbance regime. [3, 5]



Photo credits: Rick Prather (left); Aaron Shiels (right)

Partnerships

U.S. Forest Service International Institute of Tropical Forestry | Smithsonian ForestGEO | Luquillo Critical Zone Observatory | Department of Energy Next Generation Ecosystem Experiments-Tropics Research Program | PhenoCam Network | University of Puerto Rico





Synthesis

Luquillo LTER contributes to Smithsonian's Center for Tropical Forest Science – Forest Global Earth Observatories which has resulted in numerous cross-site publications comparing forest dynamics at Luquillo to other tropical, temperate, and boreal sites. This collaboration has important implications for understanding controls of biodiversity and for forest management.

Understanding how participating in the LTER Program has changed the nature of scientists.

Luquillo LTER spearheaded the effort by studying a large cross-section of the LTER community and initiating a collection of in-depth analyses of the challenges and accomplishments of long term ecological research.



Photo credits: USFS/Joel Olivencia (left); LUQ LTER (top, bottom)

Luquillo and Florida Coastal Everglades LTER scientists are collaborating

to edit a special issue of *Ecosphere* called “Resistance, Resilience, and Vulnerability to High

Energy Storms: A Global Perspective”. This effort involves cross-site comparisons with coastal Australia, Dominican Republic, Florida, Guadalupe and Dominica, Louisiana, Mexico, Puerto Rico, and Taiwan.

Data Accessibility

The LUQ LTER Information Management System (LIMS) is a product of continuous collaboration between LUQ LTER information managers and the LTER research community. LIMS complies with LTER Network policies and uses software that serves as both an information management system and a tool for data discovery. Data are posted on the LIMS website and deposited with the Environmental Data Initiative repository.

Broader Impacts

Journey to El Yunque. Teachers use a 4-week bilingual middle school curriculum unit called Journey to El Yunque to engage students. Using LUQ LTER data, students analyze the effects of hurricanes and human activity on Luquillo's ecosystems. The curriculum has leveraged funding from NSF and the Department of Education to investigate modes of student learning, among other things.



Schoolyard LTER. Public and private partners engage schoolteachers and students in [Data Jams](#). Data Jams supports students in exploring, analyzing, and summarizing long term data about the environment. Students then communicate their discoveries to non-scientific audiences through artistic means like dance, poetry, and baking. Teachers who successfully implement the Data Jam are invited to bring their students to El Verde Field Station to learn basic field protocols related to tree growth, soil, and hydrology.

Research and Career Development for Undergraduate Students and Post-baccalaureate Interns. Students involved in Luquillo's Research Experience for Undergraduates (REU) program are incorporated into summer mentored research programs at El Verde Field Station. Natural Resource Career Tracks, funded by USDA-NIFA, engages students from Puerto Rico in summer internships and other career enhancement activities at USDA National Forests and other USDA agencies.

Top Products

1. Brokaw, NVL et al. 2012. A Caribbean forest tapestry: The multidimensional nature of disturbance and response. **Oxford University Press**, New York, New York.
2. Feng, X et al. 2017. Improving predictions of tropical forest response to climate change through integration of field studies and ecosystem modeling. **Global Change Biology**. doi: 10.1111/gcb.13863
3. González, G, Willig, MR, Waide, RB 2013. Advancements in the understanding of spatiotemporal gradients in tropical landscapes: a Luquillo focus and global perspective. **Ecological Gradient Analyses in a Tropical Landscape**. Willig, MR; Waide, RB, eds. Ecological Bulletins 54. Hoboken, NJ: Wiley-Blackwell.
4. McDowell, WH et al. 2013. Interactions between lithology and biology drive the long-term response of stream chemistry to major hurricanes in a tropical landscape. **Biogeochemistry**. doi: 10.1007/s10533-013-9916-3
5. Miller, PW et al. 2018. A 42-Year inference of cloud base height trends in the Luquillo Mountains of northeastern Puerto Rico. **Climate Research**. doi: 10.3354/cr01529
6. Schowalter, TD et al. 2017. Post-hurricane successional dynamics in abundance and diversity of canopy arthropods in a tropical rainforest. **Environmental Entomology**. doi: 10.1093/ee/nvw155
7. Shiels, AB et al. 2015. Cascading effects of canopy opening and debris deposition from a large-scale hurricane experiment in a tropical rainforest. **BioScience**. doi: 10.1093/biosci/biv111
8. Uriarte, M et al. 2012. Multidimensional trade-offs in species responses to disturbance: implications for successional diversity in a subtropical forest. **Ecology**. doi: 10.2307/23144033
9. Willig, MR et al. 2019. Long-term population trends in El Yunque National Forest (Luquillo Experimental Forest) do not provide evidence for declines with increasing temperature or the collapse of food webs. **PNAS**. doi: 10.1073/pnas.1820456116
10. Wood, T.E., and W.L. Silver. 2012. Strong spatial variability in trace gas dynamics following experimental drought in a humid tropical forest. **Global Biogeochemical Cycles**. doi: 10.1029/2010GB004014



McMurdo Dry Valleys LTER

The polar desert landscape of the McMurdo Dry Valleys is a mosaic of inter-connected arid soils, glaciers, streams, and ice covered, closed basin lakes. With less than 10 cm water equivalent per year in precipitation, an annual mean temperature of -18°C , and no vascular plants, food webs are relatively simple. While microbial, algal, and invertebrate communities in the streams, soils, and glaciers are inactive during the austral winter, the ice covered lake communities are active year round.

The McMurdo Dry Valleys (MCM) LTER has explored the physical controls on ecosystem structure and function, the influence of past climate legacies (e.g., glaciation and lake inundation/recession) on the ecosystem, the interactions of climate legacies with contemporary biotic and physical processes, responses to climate warming in the region and associated increases in ecosystem connectivity. Current research is focused on how ecological resistance and resilience modulates the response of communities and ecosystems to amplified connectivity.



Between 2008-2018:

14 investigators

15 institutions represented

115 graduate students



Freshwater

Principal Investigator:

Michael Gooseff

University of Colorado, Boulder

Est. 1993

Funding Cycle:

LTER V

NSF Program:

Geosciences / Office of Polar Programs



Key Findings

A single extreme summer has long lasting impacts on the McMurdo Dry Valleys ecosystem. During a decadal cooling period, productivity and hydrological connectivity synchronously decreased among terrestrial and aquatic ecosystems. As summer air temperatures and solar radiation stabilized in the following decade, the ecosystem moved back toward pre-cooling period conditions but in an asynchronous manner. This was due in part to the fact that the end of the cooling period was punctuated by the highest glacial melt summer on record. [Products 1-4]



Connectivity matters in a rapidly changing environment.

Record melt and thaw events over the past decade have increased the physical connectivity of the McMurdo Dry Valleys ecosystem.

Researchers at MCM LTER have tested hypotheses that focus on responses, such as

increased biogeochemical cycling and changes in biodiversity.

These studies suggest that landscape morphology is changing as permafrost thaws, and that biological communities are indeed responding to altered climatic conditions (e.g., high and low flow controls on stream benthic mat abundance). [5-7]

Significance of lake moats.

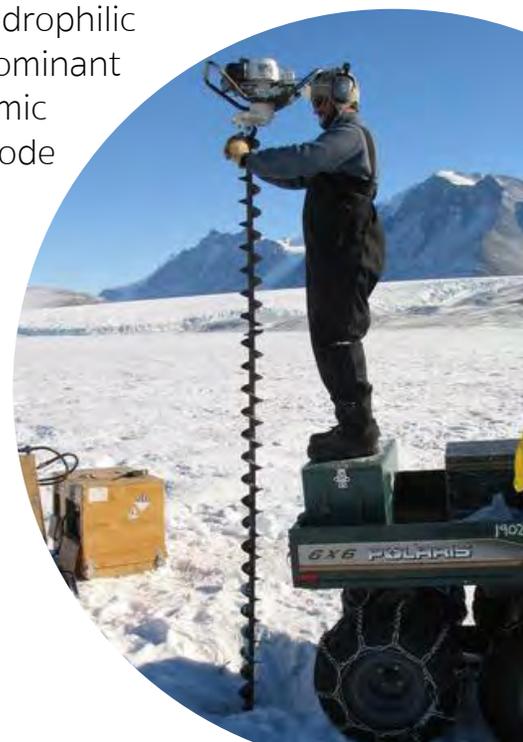
In the austral summer, the shallow margins of ice-covered lakes melt, forming moats around the permanent ice covers of the lakes. Waters here interact with streams, soils, and the atmosphere (unlike those under the permanent ice).

Recent study of these moats has uncovered these as the locations of the highest biomass per unit area in the dry valleys landscape.



Observed and experimentally induced changes in climate and hydrology are altering soil communities in the McMurdo Dry Valleys.

Soil invertebrate communities in long term monitoring plots are responding to long term and seasonal changes in temperature and water availability, with key taxa exhibiting distinct responses. These changes are favoring rarer hydrophilic taxa, while the dominant species, an endemic free-living nematode which prefers cold dry soils, is declining in monitoring and experimentally manipulated plots. [1,8]



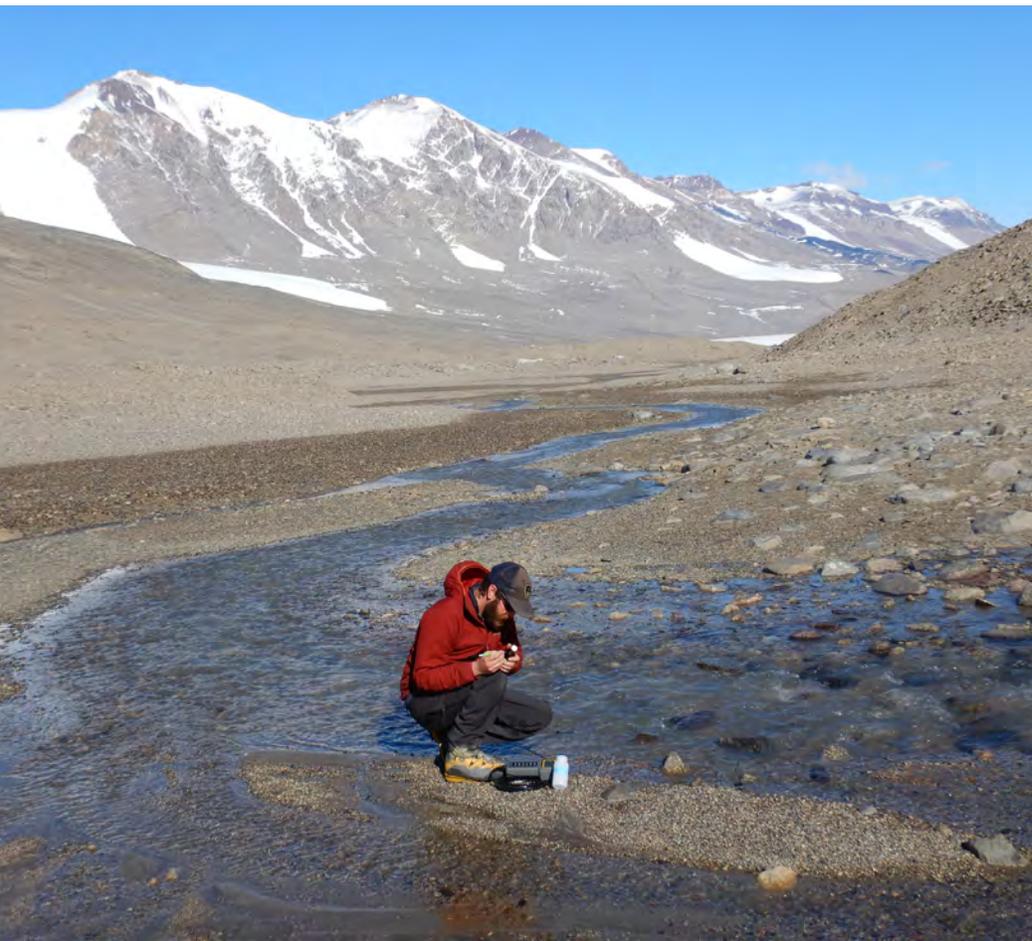
Phytoplankton community diversity and function are sensitive to nutrients and light.

Photosynthetic and mixotrophic eukaryotes are the dominant primary producers in the stratified water columns of the dry valleys lakes. Nutrient amendment experiments have shown that growth of chlorophytes, an obligate photosynthetic phytoplankton group, are stimulated by the addition of nitrogen or phosphorus in Lake Fryxell and nitrogen in Lake Bonney. Conversely, when communities are transplanted to the high light environment of open water moats, chlorophyte abundance and photosynthetic activity declined significantly. These results indicate that climate-related changes have conflicting impacts on phytoplankton communities (increased nutrient input versus lake level rise/expanding moats). [9,10]

Synthesis

Metacommunity Synthesis. The MCM LTER has been an intellectual leader in collaborative efforts to understand the impacts of metacommunity theory and extend its applications to understanding diversity patterns in a changing world. The resulting Metacommunities Synthesis Group, funded through the LTER Network Office, has produced a series of high profile papers and strengthened connections between NEON and the LTER Network.

Resilience on the Southern Continent. In 2016, MCM LTER published a special set of 3 papers in *BioScience* that compared the basic ecology of the two Antarctic LTER sites and the alignment of their responses to an anomalous summer. These collaborative papers demonstrated that across terrestrial and marine ecosystems, Antarctic communities are synchronously responding to the changes observed to date.



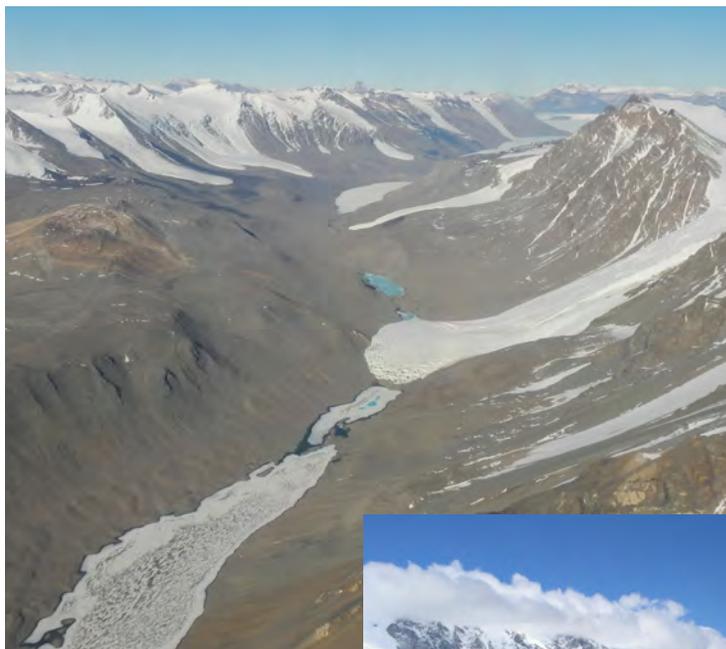
Data Accessibility

The MCM LTER database includes data from investigators at MCM LTER, collected as early as 1987, from all related field studies and laboratory analyses. These data are hosted in the [MCM online database](#) and through the Environmental Data Initiative (EDI) repository. The philosophy that data and metadata must be quickly and freely made available is instilled in students and postdocs throughout their time at MCM LTER.

Broader Impacts

Bringing an extraordinary experience home.

Access to Antarctica is limited, even for the MCM science team. Therefore, researchers have developed ways of engaging with this remote site through multimedia and personal storytelling to convey lessons learned to students around the world. Outreach is facilitated by the ability to conduct web conferences from Antarctica, news and popular media-initiated products, and through public, in-person presentations after researchers return from Antarctica.



The Lost Seal. The children's book *The Lost Seal* was the first to be published in the LTER Schoolyard book series. The book provided lessons about scientific field work and initiated a wave of new products from other LTER sites



across the Network. With leveraged funding, the book has been translated into several languages and distributed around the world.

Human Connections to the 7th Continent.

Despite Antarctica having no indigenous human population, the rich history of exploration and scientific endeavor provides a wealth of context for this ecosystem as it is understood today. With a particular focus on the theme of disturbance, environmental history research efforts focus on the human connections to the dry valleys from their discovery in the early 1900s to the modern era of drones and satellites as scientific tools.

Photo credits: MCM LTER (above and cover)

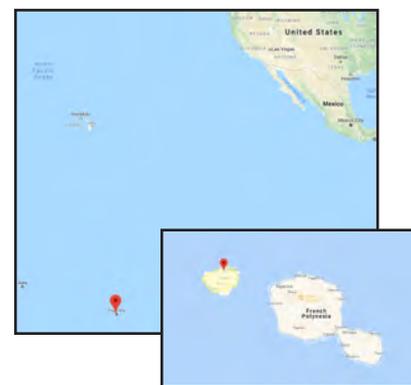
Top Products

1. Gooseff, MN et al. 2017. Decadal ecosystem response to an anomalous melt season in a polar desert in Antarctica. **Nature Ecology & Evolution**. doi:10.1038/s41559-017-0253-0
2. Nielsen, et al. 2012. The ecology of pulse events: insights from an extreme climatic event in a polar desert ecosystem. **Ecosphere**. doi: 10.1890/ES11-00325.1
3. Šabacká, et al. 2012. Aeolian flux of biotic and abiotic material in Taylor Valley, Antarctica. **Geomorph**. doi: 10.1016/j.geomorph.2011.12.009
4. Michaud, et al. 2012. Cyanobacterial diversity across landscape units in a polar desert: Taylor Valley, Antarctica. **FEMS Microbio. Ecol.** doi: 10.1111/j.1574-6941.2012.01297.x
5. Stanish LF et al. 2012. Extreme streams: flow intermittency as a control on diatom communities in meltwater streams in the McMurdo Dry Valleys, Antarctica. **Canadian J. Fisheries Aquatic Sci.** doi: 10.1139/F2012-022
6. Fountain, et al. 2014. The McMurdo Dry Valleys: A landscape on the threshold of change. **Geomorph**. doi: 10.1016/j.geomorph.2014.03.044
7. Okie, et al. 2015. Niche and metabolic principles explain patterns of diversity and distribution: theory and a case study with soil bacterial communities. **Proc. Royal Soc.-B**. doi: 10.1098/rspb.2014.2630
8. Andriuzzi et al. 2018. Observed trends of soil fauna in the Antarctic Dry Valleys: early signs of shifts predicted under climate change. **Ecology**. doi: 10.1002/ecy.2090.
9. Morgan-Kiss et al. 2016. Photoadaptation to the polar night by phytoplankton in a permanently ice-covered Antarctic lake. **Limnol. Oceanogr.** doi: 10.1002/lno.10107
10. Li et al. 2019. Influence of environmental drivers and potential interactions on the distribution of microbial communities from three permanently stratified Antarctic lakes. **Front Microbiol.** doi: 10.3389/fmicb.2019.01067.

Moorea Coral Reef LTER

The Moorea Coral Reef (MCR) LTER program studies the coral reef ecosystem surrounding the island of Moorea, French Polynesia in the central South Pacific. Moorea Coral Reef LTER research is dedicated to understanding coral reef function and how this is affected by natural and human forces. In its first 15 years, MCR LTER has altered scientific paradigms regarding how coral reef ecosystems respond to disturbances such as hurricanes, chronic stressors from local human activities (eutrophication, fishing), and global change (ocean acidification, rising ocean temperature).

Moorea Coral Reef LTER has uncovered key attributes that govern contemporary reef community resilience and factors that will shape future communities in a warmer, more acidic ocean. Through conceptually-driven time series and process measurements, field and mesocosm experiments, and modeling, MCR researchers have developed a deep mechanistic understanding of ecosystem dynamics and functioning, and are positioned to forecast the effects of intensifying global change and the expanding human footprint on oceanic coral reef ecosystems.



Between 2008-2018:

42 investigators

14 institutions represented

84 graduate students



Coastal

Principal Investigator:

Russell J. Schmitt

University of California,
Santa Barbara

Est. 2004

Funding Cycle:

LTER III

NSF Program:

Geosciences /
Division of Ocean Sciences /
Biological Oceanography



Key Findings

Ocean acidification (OA) is an emerging threat.

Researchers at MCR LTER have been at the forefront of evaluating how OA will affect the structure and function of future reefs. The ecosystem engineers that structure coral reefs – stony corals and calcified algae – are uniquely threatened by low seawater pH. Using time series data to determine experimental conditions, researchers have tested for coral susceptibility to low seawater pH, the dependence of these responses on space, time, and functionality scales, and the implications for future coral reefs. [Products 1, 2]



Unprecedented resilience of coral communities.

The diverse coral community on Moorea's outer reefs has repeatedly shown a remarkable ability to recover rapidly following massive

disturbances. In the last

decade, a predator outbreak and cyclone devastated coral across the seascape, yet recovery was more rapid than has been observed anywhere in the world. Moorea Coral Reef LTER researchers have gained critical insights into the processes, connectivities, and feedbacks governing coral reef resilience. This has provided the basis for general management strategies to help restore and strengthen coral reef community resilience. [1-3]

Coral reefs are vulnerable to disturbance-induced regime shifts.

Reefs worldwide have abruptly and increasingly shifted from coral to seaweed dominated communities.

Experiments at MCR LTER revealed that a large disturbance can cause a coral reef to flip to seaweeds indefinitely. Experiments and models showed that multiple stable states (e.g. corals or seaweeds) can continue to thrive under the same levels of herbivory. They also discovered that the seaweed state is stabilized by the development of structural and chemical defenses that reduce the palatability of mature (but not juvenile) algae [6].

Microbes and the future of coral reef function.

The powerhouse mutualism between the coral animal and its symbiotic dinoflagellate algae is the backbone of coral reef ecosystems. Moorea Coral Reef LTER research has produced counter-intuitive results, specifically that flexibility with respect to symbionts does not automatically make corals resilient – a finding that has had profound implications for understanding the susceptibility of coral colonies to stress. Similarly, MCR LTER researchers have shown that major feedbacks involving other microbes affect coral health, particularly bacteria key to the dynamic nutrient cycling on reefs. [7-8]





Synthesis

Alternative futures for coral reefs. The MCR LTER has played a global leadership role in synthetic efforts to understand the state of coral reefs and their future in warmer, more acidic oceans. The extraordinary resilience of Moorea’s reefs has motivated collaborations with the National Center for Ecological Analysis and Synthesis (NCEAS) to identify winners and losers among coral fauna, and more recently, synthesis work at the Powell Center to address reef “oases”. Multiple international efforts through the Okinawa Institute of Science and Technology have explored the roles of recruitment and connectivity in fueling reef

resilience. Core time series data on biological, physical, and chemical conditions around Moorea have been integrated in MCR-led syntheses. These projects addressed dynamic variation in seawater pH, the global threats of ocean acidification and their scale-dependence, reef resilience, and variation in coral growth rates [9].

The global human footprint on coral reefs. Moorea Coral Reef LTER investigators and MCR time series datasets have contributed to multiple synthesis projects on the relationship between coral reef biodiversity and human activities from regional to global scales [10].



Data Accessibility

Since the site was established in 2004, the MCR LTER data repository has managed a publicly accessible online catalog of core data. Data are uploaded to the the Environmental Data Initiative (EDI) repository, including links between datasets and publications. Core data are also shared publicly in databases such as BioTIME (Dornelas et al. 2018. *Global Ecology and Biogeography*. 27: 760-786) and the Coral Traits Database (Madin et al. 2017. *Scientific Data*. 4: 170-174).

Partnerships

University of California, Santa Barbara (UCSB) | California State University Northridge (CSUN) | UC Office of the President



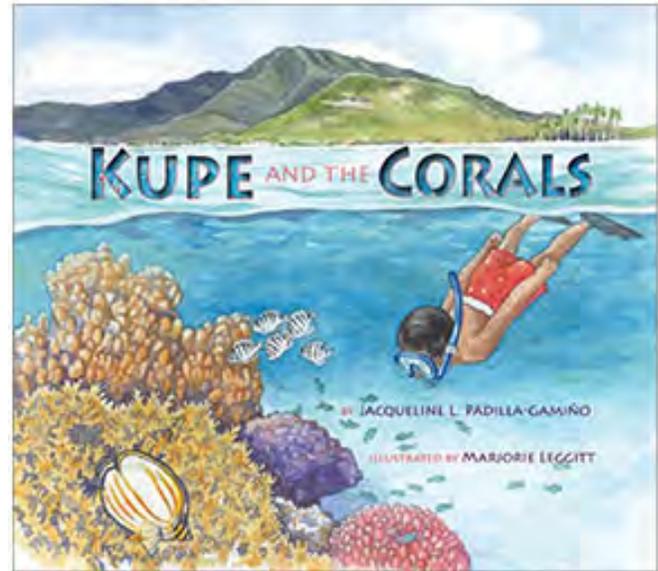
Broader Impacts

From the classroom to the reef. Each year, undergraduate students mentored by MCR LTER investigators and graduate students (192 since 2008) spend three months conducting subtidal research, working with oceanographic instruments and sensors, and learning the logistics of field operations. Surveys indicate that >90% of these students go on to pursue advanced degrees in the environmental sciences.

Building science literacy. The MCR LTER Research Experience for Teachers (RET) program enables grade 3-12 teachers in California to increase their marine science knowledge through sponsored teacher workshops. Since 2008, 7 teachers have worked directly with MCR researchers, and 3 participated in a two week oceanographic cruise around Moorea.

Magnet school partnership. Since 2005, the MCR LTER Schoolyard Program has partnered with teachers and 1,500+ students at Washington Elementary STEM Magnet School in Pasadena, CA (student body 87% socioeconomically disadvantaged; 36% English language learners). Investigators work with teachers to develop classroom materials based on MCR science and data. Each year, 5th grade

students from Washington Elementary visit UC Santa Barbara for a science exploration day that includes hands-on learning at the REEF (Research Experience and Educational Facility), presentations, and active learning exercises led by MCR LTER graduate students.



Kupe and the Corals. The children's book, *Kupe and the Corals*, tells the story of a young Tahitian boy who, after capturing a coral larva one night, begins a voyage of scientific and cultural discovery. The book has been published in English, Spanish, French, Hawaiian, Tahitian, and Paumotu for use throughout southern California, Hawaii, and French Polynesia.

Top Products

1. Comeau, S et al. 2015. Ocean acidification accelerates dissolution of experimental coral reef communities. **Biogeosciences**. doi: 10.5194/bg-12-365-2015
2. Comeau, S et al. 2016. Framework of barrier reefs threatened by ocean acidification. **Global Change Biology**. doi: 10.1111/gcb.13023
3. Holbrook, SJ et al. 2018. Recruitment drives spatial variation in recovery rates of resilient coral reefs. **Scientific Reports**. doi: 10.1038/s41598-018-25414-8
4. Edmunds, J et al. 2018. Density-dependence mediates coral assemblage structure. **Ecology**. doi: 10.1002/ecy.2511
5. Adam, TC et al. 2011. Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. **PLOS ONE**. doi: 10.1371/journal.pone.0023717
6. Schmitt, RJ et al. 2019. Experimental support for multiple attractors on coral reefs. **PNAS**. doi: 10.1073/pnas.1812412116
7. Putnam, HM et al. 2012. Endosymbiotic flexibility associates with environmental sensitivity in scleractinian corals. **Proceedings of the Royal Society B – Biological Sciences**. doi: 10.1098/rspb.2012.1454
8. Nelson, CE et al. 2013. Coral and macroalgal exudates vary in neutral sugar composition and differentially enrich reef bacterioplankton lineages. **ISME Journal**. doi: 10.1038/ismej.2012.161
9. Edmunds, PJ et al. 2016. Integrating the effects of ocean acidification across functional scales on tropical coral reefs. **Bioscience**. doi: 10.1093/biosci/biw023
10. Cinner, JE et al. 2016. Bright spots among the world's coral reefs. **Nature**. doi: 10.1038/nature18607

Photo credits: MCR LTER; Russell Schmitt (bottom page 2); Marjorie Leggitt (above)



Photo credit: Jacob Strock

Northeast U.S. Shelf LTER

The Northeast U.S. Shelf (NES) LTER is co-located with the highly productive Northeast U.S. Continental Shelf Large Marine Ecosystem, utilized for fisheries, recreation, energy, and transportation. The site's broad-scale studies span the Mid-Atlantic Bight and the Gulf of Maine, with a focal cross-shelf transect extending ~150 km southward from the Martha's Vineyard Coastal Observatory (MVCO) to just beyond the Ocean Observatories Initiative (OOI) Pioneer Array at the shelf break. The region is experiencing faster-than-average warming and other impacts from environmental variability and human activity.

Although patterns of ecosystem change over seasons to decades have been documented, key mechanisms linking changes in the physical environment, planktonic food webs, and higher trophic levels remain poorly understood. Northeast U.S. Shelf LTER research integrates observations, experiments, and models to understand and predict how planktonic food webs are changing, and how those changes impact the productivity of higher trophic levels.



At present:

18 investigators

5 institutions represented

13 graduate students



Marine

Principal Investigator:

Heidi M. Sosik

Woods Hole Oceanographic
Institution

Est. 2017

Funding Cycle:

LTER I

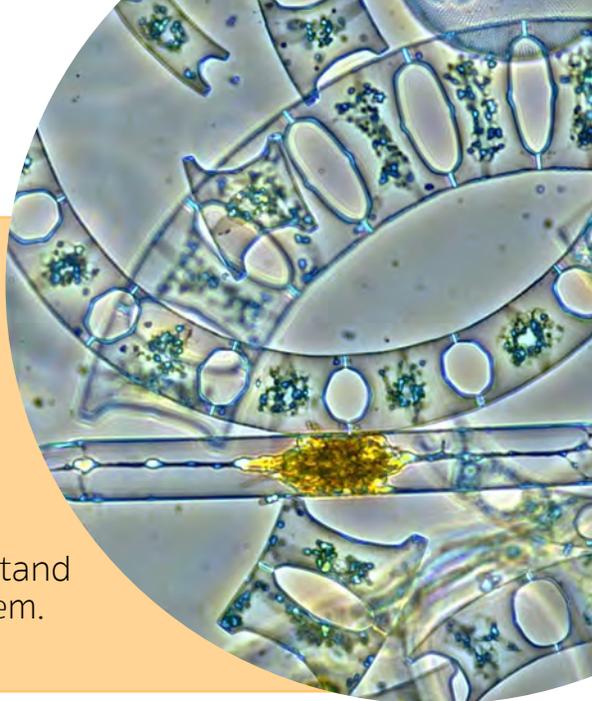
NSF Program:

Geosciences / Division of
Ocean Sciences / Biological
Oceanography



Key Findings

Shifts in phytoplankton phenology are associated with warming trends. Phytoplankton bloom dynamics at Martha's Vineyard Coastal Observatory (MVCO) are sensitive to temperature variability on both seasonal and decadal scales. Multi-year sampling has shown that the genetic background of phytoplankton is diverse and changes rapidly in coastal shelf waters. Ongoing NES LTER observations emphasize the complementary nature of multiple approaches (sequencing, imaging, and flow cytometry) to better document and understand changes in plankton diversity and how it impacts the ecosystem. [Products 1-4]



Spatiotemporal dynamics in microzooplankton. Thanks to automated imaging approaches developed by NES LTER researchers, unprecedented insight has been gained into variations in microzooplankton biomass and diversity across a broad range of space and time scales [5]. In addition, studies in Narragansett Bay documented strong microzooplankton grazing pressure on phytoplankton throughout the year, irrespective of season [6].

Decadal changes in zooplankton abundance and fish distributions.

Long term changes in zooplankton abundance and biovolume were documented prior to the funding of NES LTER. The distributions of many fish species in the Mid-Atlantic Bight are shifting northward in the warming ocean. Dominant species of zooplanktivorous forage fishes have interannual, seasonal, and species-specific diet preferences. It remains unresolved how decadal changes in zooplankton influence this higher trophic level. [7-9]

Improved spatial resolution for coupled physical-biological models. NOAA has selected NES LTER PI Changsheng Chen's Finite Volume Community Ocean Model (FVCOM) as the basis of the U.S. Coastal Forecast System.

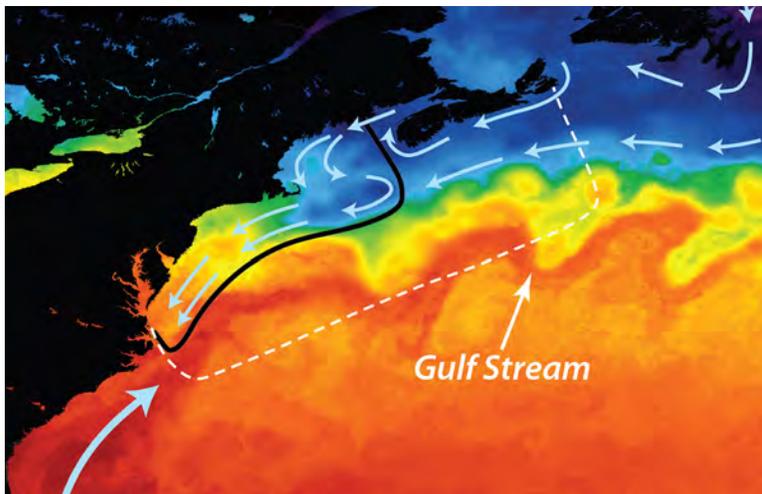
Seasonal switch in carbon cycle efficiency. Initial results from transect cruises indicate that the ratio of net community production to gross primary production peaks onshore in the winter, but offshore during summer. The ratio is a measure of carbon cycle efficiency.



Synthesis

Initiated cross-site comparisons with other pelagic marine sites. Investigators from NES LTER co-organized a special session at the 2018 LTER All Scientists Meeting with 3 other oceanic sites. This collaboration is also expected to produce standardized protocols.

Co-authored work on the status and future prospects for the 100+ ILTER coastal and marine sites. As part of ILTER, NES LTER is already contributing Essential Ocean Variables to global efforts (as recommended by Framework for Ocean Observation). This work has drawn attention to new technologies and the ongoing importance of coordinated observational activities between LTER sites [10].



Data Accessibility

The primary goals of NES LTER information management are to facilitate continued public access to LTER data and metadata. Ship-provided data from transect cruises can be found in the Rolling Deck to Repository (R2R) and broad scale cruise data is deposited with NOAA NEFSC partners. Both types of data are ultimately archived at the National Center for Environmental Information (NCEI).

Data from post-cruise analyses will be shared as curated data products via the Environmental Data Initiative repository (EDI). Physical oceanographic model data are stored in the Northeast Coastal Ocean Forecast System (NECOFS). Code for the local information management system (IMS) is available in GitHub repositories online.

Photo credits: U.S. LTER

Partnerships

NOAA Northeast Fisheries Science Center (NEFSC) | Ocean Observatories Initiative (OOI) | Martha's Vineyard Coastal Observatory (MVCO) | Northeast Coastal Ocean Forecast System (NECOFS)



Broader Impacts

Ecosystem-based management. Researchers at NES LTER partners with NOAA Northeast Fisheries Science Center (NEFSC) for collaborative research pertinent to managing living marine resources and to integrate LTER data with the longer term NOAA datasets. NEFSC scientists serve on LTER graduate student dissertation committees.



Northeast U.S. Shelf LTER engages undergraduates from many backgrounds. Data collected by NES LTER researchers during laboratory and open sea research are used in undergraduate courses, such as Wellesley College's "Chem 103: Elements and the Environment," which teaches students from all majors scientific literacy through an environmental lens.

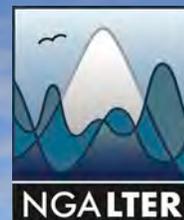


Professional development for teachers. The NES LTER Schoolyard program engages regional teachers in webinars focused on science and data literacy. Teachers are encouraged to join research cruises and enroll their students in the NES LTER Data Jam competition. Researchers from NES LTER also present annually at the Massachusetts Marine Educators Annual Meeting.



Top Products

1. Peacock, EE et al. 2014. Parasitic infection of the diatom *Guinardia delicatula*, a recurrent and ecologically important phenomenon on the New England Shelf. **Marine Ecology Progress Series**. doi: 10.3354/meps10784
2. Hunter-Cevera, KR et al. 2016. Physiological and ecological drivers of early spring blooms of a coastal picophytoplankter. **Science**. doi:10.1126/science.aaf8536
3. Rynearson, T et al. 2018. Impacts of microdiversity on succession and organism interactions in the plankton. **2018 Ocean Science Meeting**, Portland, OR
4. Sosik, HM. 2018. Sequencing, cytometry, and imaging provide complementary assessment of plankton communities in the MVCO time series. **ICES Annual Science Conference 2018**, Hamburg, Germany
5. Brownlee, EF et al. 2016. Microzooplankton community structure investigated with imaging flow cytometry and automated live-cell staining. **Marine Ecology Progress Series**. doi: 10.3354/meps11687
6. Lawrence, C. and S. Menden-Deuer. 2012. Drivers of protistan grazing pressure: seasonal signals of plankton community composition and environmental conditions. **Marine Ecology Progress Series**. doi: 10.3354/meps09771
7. Morse, RE et al. 2017. Distinct zooplankton regime shift patterns across ecoregions of the U.S. Northeast continental shelf Large Marine Ecosystem. **Journal of Marine Systems**. doi: 10.1016/j.jmarsys.2016.09.011
8. Kleisner, KM et al. 2016. The Effects of Sub-Regional Climate Velocity on the Distribution and Spatial Extent of Marine Species Assemblages. **PLOS ONE**. doi: 10.1371/journal.pone.0149220
9. Suca, JJ et al. 2018. Feeding dynamics of Northwest Atlantic small pelagic fishes. **Progress in Oceanography**. doi: 10.1016/j.pocean.2018.04.014
10. Muelbert, JH et al. 2019. ILTER - the International Long-Term Ecological Research network as a platform for global coastal and ocean observation. **Frontiers in Marine Science**. doi: 10.3389/fmars.2019.00527



Northern Gulf of Alaska LTER

Photo credit: Ana Anguilar-Islas

The Northern Gulf of Alaska (NGA) LTER is based in the coastal Gulf of Alaska and mobilizes field expeditions from the Seward Marine Center of the University of Alaska, Fairbanks. The program seeks to understand how this subarctic shelf system generates the high productivity that sustains one of the world's largest commercial fisheries, as well as iconic seabird and marine mammal species. Ocean physics in the Gulf of Alaska have been monitored for nearly 50 years, and chemistry and biology have been recorded for the last 20 years. Together, this provides foundational information about the structure and function of this subarctic ecosystem.

Scientists in the region have developed a solid understanding of annual cycles and are beginning to appreciate the scales and drivers of observed interannual variability (i.e. ENSO, marine heat waves). Through sustained measurements, NGA LTER aims to determine how resiliency arises, how emergent properties provide community level structure, and whether longer term environmental changes will impact this resiliency. Findings will inform biological resource management in the Gulf of Alaska.



At present:

15 investigators

6 institutions represented

9 graduate students



Marine

Principal Investigator:

Russ Hopcroft

University of Alaska, Fairbanks

Est. 2017

Funding Cycle:

LTER I

NSF Program:

Geosciences / Division of Ocean Sciences



Key Findings

Stratification is changing. The coastal Gulf of Alaska water column is becoming progressively more stratified — the entire water column is warming, but more rapidly at the surface than near the seafloor, while near surface waters are becoming fresher. This is due to multiple factors including the air-sea heat flux, ocean heat flux convergences, the stabilizing influence of runoff, the destabilizing effects of cooling and vertical mixing, and the wind driven cross-shelf buoyancy flux. Stratification impacts the water column mixing in winter that helps reset the shelf for the next season's biological production. Therefore, the concentration and composition of the phyto- and zooplankton community shows direct and indirect connections to the thermal conditions of the Gulf of Alaska shelf. These far reaching implications for upper trophic levels could only be detected using a high quality, multi-decade dataset. [Products 1-3]

Anomalous warming in 2015-16 led to profound reorganization of lower trophic levels. Reductions in primary producer average cell size and biomass followed the 2015-2016 warming, as did corresponding reductions at higher trophic levels. In addition, southern zooplankton species of smaller body size invaded the region and anomalous increases in gelatinous zooplankton population were observed. These changes, which could represent a window into the future of the Northern Gulf of Alaska, were associated with widespread seabird mortality, reduced forage fish abundance, and range shifts or reductions in commercially important groundfish species. The anomalous nature of the warm period was only evident in the context of long term observations establishing the typical subarctic character of this pelagic ecosystem. [3-5]

Iron-deficient surface waters are common during spring. Although glacial input leads to high iron concentrations during summer and fall within the narrow Alaska Coastal Current, the ratio of iron to nitrate over the Northern Gulf of Alaska shelf in spring can be low enough to lead to nutritional stress in diatoms. This mismatch in essential nutrients likely affects phytoplankton community evolution during the spring bloom [6].



Modeling illuminates eddy-induced cross-shelf transport. Modeling at NGA LTER investigates how the complex interplay between the strongly seasonal freshwater discharge at the coast and offshore eddies controls horizontal gradients of limiting nutrients (nitrate and iron). This work builds on previous modeling studies in the region that utilized Seward Line observations to improve the accuracy of simulated physical and biogeochemical fields. Moreover, previous models quantified the importance of eddy induced entrainment of shelf iron to offshore primary production, which extends to phyto- and zooplankton community structure. [7-9]

Photo credit (below): Anne-Lise Ducluzeau; <https://anneliseducluzeau.com>



Synthesis

As a new LTER site, NGA LTER has only recently become engaged in cross-site synthesis. However, during its early involvement with the Global Ocean Ecosystem Dynamics (GLOBEC) program, the Northern Gulf of Alaska was compared to the LTER sites that are now the California Current Ecosystem, Northeast U.S. Shelf, and Palmer Station. Discussions at the recent LTER All Scientists' Meeting indicate that several cross-site comparisons are expected in the near future.



Data Accessibility

Much of the legacy data from the Seward Line and the Gulf of Alaska 1 (GAK1) oceanographic station are already available online through the Alaska Ocean Observing System (AOOS), with even earlier GLOBEC data within the Biological and Chemical Oceanography Data Management Office (BCO-DMO). Our accumulated knowledge is allowing more judicious evaluation of the legacy data and, where possible, reanalysis of the original data sets. As a new site, our new website and portal (Axiom) are still undergoing active development.

Photo credit: NGA LTER

Broader Impacts

Graduate education. During the Northeast Pacific Program (NEP) GLOBEC, the Northern Gulf of Alaska produced 12 graduate students. Nine additional graduate students will be involved in the project by the end of the 2019 season.

From science to fiction. Associated projects (e.g., Gulf Watch Alaska and North Pacific Research Board's Gulf of Alaska Project) have produced web content and videos outlining the basic ecological function of the region's ecosystem. This research formed the basis of "pH. A novel" by Nancy Lord.

Partnerships

NOAA | GLOBEC | Northern Pacific Research Board (NPRB) | Exxon Valdez Oil Spill Trustee Councils (GAK1)

Bringing the ocean to the classroom. By participating in NOAA's teacher-at-sea program, NGA LTER is helping spread knowledge about the region's ecosystems and scientific endeavors into the K-12 system.



The Legacy of Exxon Valdez. The NGA LTER continues the ecosystem monitoring that is a key legacy of the 1989 Exxon Valdez oil spill. The data have helped distinguish between the effects of the oil spill on the Gulf of Alaska ecosystem and intrinsic and climate-driven variability.

Engaging tourists and residents. Site researchers contributed stories to "Delta Sound Connections," an annual natural history and science publication of the Prince William Sound Science Center, which reaches visitors at dozens of activity hotspots in Alaska.

Top Products

1. Kelley, J. 2015. An examination of hydrography and sea level in the Gulf of Alaska. **M.S. Thesis**, University of Alaska Fairbanks.
2. Janout, M et al. 2010. On the nature of winter cooling and the recent temperature shift on the northern Gulf of Alaska shelf. **J. Geophys. Res.** doi:10.1029/2009JC005774
3. Batten, SD et al. 2017. Interannual variability in lower trophic levels on the Alaskan Shelf. **Deep-Sea Res. II.** doi: 10.1016/j.dsr2.2017.04.023
4. Strom, SL et al. 2016. Spring phytoplankton in the eastern coastal Gulf of Alaska: Photosynthesis and production during high and low bloom years. **Deep-Sea Research II.** doi: 10.1016/j.dsr2.2015.05.003
5. Strom, SL et al. 2019. Microzooplankton in the coastal Gulf of Alaska: regional, seasonal and interannual variations. In press, **Deep-Sea Research II.** doi: 10.1016/j.dsr2.2018.07.012
6. Aguilar-Islas, AM et al. 2016. Temporal variability of reactive iron over the Gulf of Alaska shelf. **Deep-Sea Res. II.** doi: 10.1016/j.dsr2.2015.05.004
7. Coyle, KO et al. 2013. Zooplankton biomass, advection and production on the northern Gulf of Alaska shelf from simulations and field observations. **J. Mar. Sys.** doi: 10.1016/j.jmarsys.2013.04.018
8. Fiechter, J. et al. 2011. A data assimilative, coupled physical-biological model for the Coastal Gulf of Alaska. **Dyn. Atm. Oceans.** doi: 10.1016/j.dynatmoce.2011.01.002
9. Fiechter, J. and Moore, A.M. 2012. Iron limitation impact on eddy-induced ecosystem variability in the coastal Gulf of Alaska. **J. Mar. Sys.** doi: 10.1016/j.jmarsys.2011.09.012



North Temperate Lakes LTER

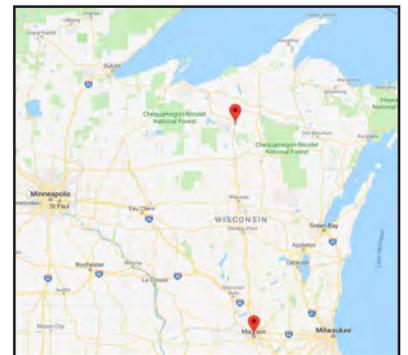
The North Temperate Lakes (NTL) LTER program studies how geographic setting, climate, and changing land use interact to shape the ecology of lakes over time. Research activities focus on 7 lakes in northern Wisconsin surrounded by forested landscape and 4 lakes in southern Wisconsin in an agriculturally dominated landscape. Studies in these two distinct regions have generated new understanding of physical and ecological responses to a shifting climate, invasive species impacts, heterogeneity in water quality, and complex interactions that may lead to sudden ecosystem change. One of the world's richest long term lake datasets underpins these insights. Moving forward, NTL LTER researchers will expand on this body of work to describe, understand, and forecast shifting baselines and ecological transitions in lakes and their landscapes at local to global scales.

Between 2008-2018:

45 investigators

3 institutions represented

30 graduate students



Principal Investigator:
Emily Stanley
University of Wisconsin,
Madison

Est. 1981
Funding Cycle:
LTER VII

NSF Program:
Biological Sciences /
Division of Environmental
Biology



Key Findings

Divergent consequences of climate change.

Long term records show declining ice duration, lake warming, and increased variability in decadal lake level cycles. However, the magnitude of these physical changes, and their ecological consequences, differ substantially among lakes, including differences in warming rates, shifts in fish populations, and fluctuations in water clarity. [Products 7, 9, 10]

Anticipating regime shifts in ecosystems.

Regime shifts are large, persistent, and often abrupt changes in ecosystem structure and function that may be difficult to reverse.

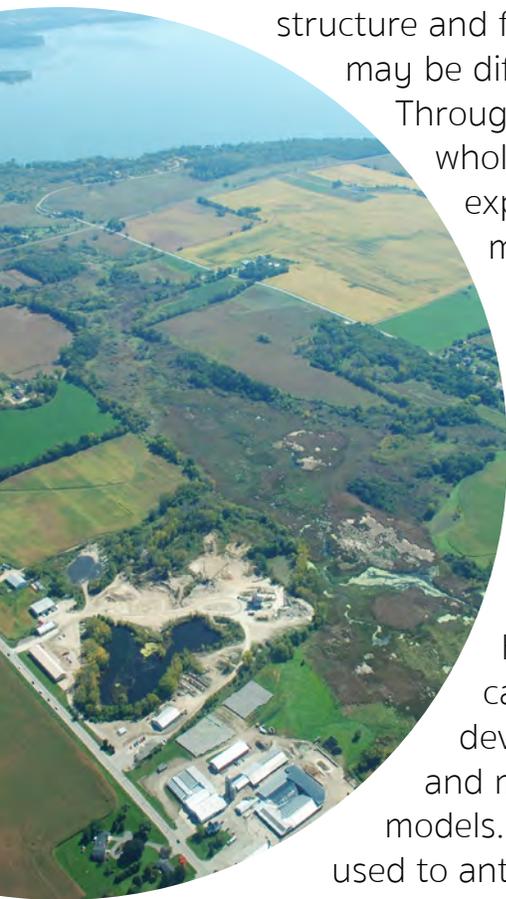
Through long term whole ecosystem experiments and measurements, NTL LTER researchers have described regime shifts involving lake eutrophication and food web structure, and have used these case studies to develop conceptual and mechanistic models. These models are used to anticipate ecosystem shifts and evaluate the utility of management actions to prevent them. [1, 3]

Lakes are major players in regional carbon cycling. Terrestrial organic carbon (C) entering lakes can be stored, sent to the atmosphere as CO₂, or passed downstream. Long term

measurements of hydrology and C were used to understand and model the fate of terrestrial C in lakes. In Wisconsin's 6,400 km² Northern Highland Lake District (NHLD), the fraction of organic C converted to CO₂ varied substantially among lakes due to hydrology. Nonetheless, lakes accounted for about 40% of C storage, although they represent only 13% of the region's area. [2, 4]

Invasive species alter food web dynamics and ecosystem services. Long term pre-invasion records provide an essential baseline for understanding invasive species effects, which can have profound consequences for ecosystems and society. In a key example, the spiny water flea invaded Lake Mendota, leading to massive declines in water quality and a loss in ecosystem services valued at \$140 million. [3, 8]

Lakes are full of diverse microbes. Although bacteria play a central role in processes affecting lake water quality, the taxa participating in these activities are largely undescribed. To address this knowledge gap, NTL LTER researchers have generated the largest freshwater microbial genome collection to date. These studies reveal a paradoxical pattern of large differences in community structure over time and among lakes, paired with the presence of specific taxa that are always present everywhere (the core lake microbiome), and communities that are surprisingly resilient to disturbance. [5, 6]





Synthesis

A global network of lake scientists. North Temperate Lakes LTER researchers are leaders in the formation of, and active participants in, the [Global Lake Ecological Observatory Network \(GLEON\)](#), a grassroots network of researchers studying lakes in a changing global environment. Hallmarks of GLEON activities include collaborative synthesis and data sharing, traceable to practices of the LTER Network.

Continental and global patterns and consequences of long term lake ice dynamics. As ice duration has shortened among NTL lakes over the past century, current and former NTL LTER researchers have led synthesis studies to provide context for local changes, generate forecasts of future changes in lake ice cover, and understand the ecological, social, and economic consequences of disappearing ice among lakes across the Northern Hemisphere [7].

Partnerships

UW-Madison's College of Letters & Sciences and Center for Limnology | AmeriFlux | NEON | GLEON | Wisconsin Department of Natural Resources | U.S. Geological Survey

Data Accessibility

Excellence in information management was a founding principle of NTL LTER. The tradition of easy data access and data sharing is complemented by the development of new tools and technologies that are also widely shared. The NTL information management system focuses on linkages among the components of ecological and social systems, whether designing data collection systems, structuring centralized databases, or executing analyses. Core NTL LTER data is used for syntheses and cross-site analyses by both NTL and non-NTL researchers. Information managers from NTL LTER lead the Environmental Data Initiative.



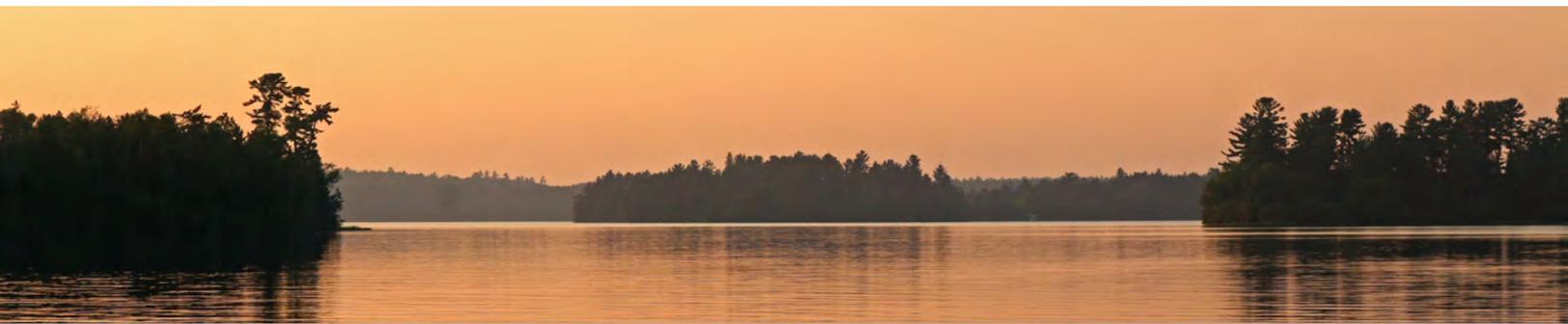
Broader Impacts

Introducing the next generation to long term lake science. The NTL Schoolyard LTER “Winter Limnology” program involves a long term partnership with five schools in the Trout Lake Station area to provide about 100 students per year (about 25% of whom are of Native American descent) with a hands on opportunity to learn about lakes and lake change. In Madison, NTL researchers and educators work with the Pre-College Enrichment Program for Learning Excellence (PEOPLE) to offer a limnology workshop for about 80 underrepresented middle and high school students per year.

Art-science nexus. Through the cross site LTER “Ecological Reflections” project, NTL’s “Drawing Water” collaborative, and the Trout Lake Station Artists-in-Residence program, NTL LTER scientists are communicating science to diverse audiences and providing a novel perspective on lakes in the landscape.

LTER science on campus. Data and research from NTL LTER are routinely used in classrooms at UW-Madison and beyond, reaching approximately 1,200 students per year. Activities include acquiring and analyzing long term datasets in undergraduate limnology classes and performing time series analysis and biogeochemical modeling in graduate seminars.

Communicating policy-relevant science. Investigators from USGS and the Wisconsin Department of Natural Resources participate actively in NTL LTER research, which facilitates long standing and substantive partnerships with these and other natural resource agencies. Examples of NTL LTER research that has informed policy and practice include lake level management in flood prone Madison lakes, preventing the spread of invasive species, and management of highly valued northern Wisconsin fisheries.



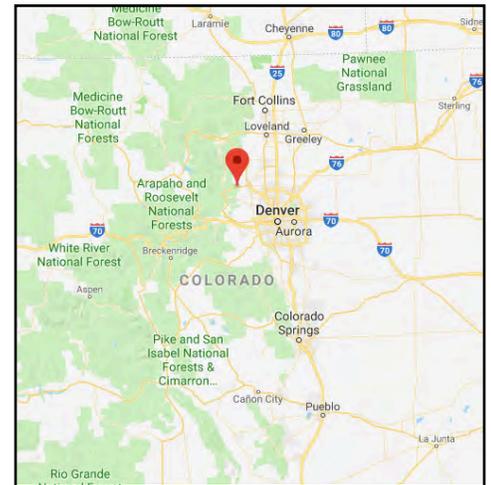
Top Products

1. Biggs, RO et al. 2008. Turning back from the brink: detecting an impending regime shift in time to avert it. **PNAS**. doi: 10.1073/pnas.0811729106
2. Buffam, I et al. 2011. Integrating aquatic and terrestrial components to construct a complete carbon budget for a north temperate lake district. **Global Change Biology**. doi: 10.1111/j.1365-2486.2010.02313.x
3. Hansen, GJA et al. 2013. Are rapid transitions between invasive and native species caused by alternative stable states, and does it matter? **Ecology**. doi: 10.1890/13-0093.1
4. Hanson, PC et al. 2014. Quantifying lake allochthonous organic carbon budgets using a simple equilibrium model. **Limnology and Oceanography**. doi: 10.4319/lo.2014.59.1.0167
5. Kara, EL et al. 2013. A decade of seasonal dynamics and co-occurrences within freshwater bacterioplankton communities from eutrophic Lake Mendota, WI, USA. **The ISME Journal**. doi: 10.1038/ismej.2012.118
6. Newton, RJ et al. 2011. A guide to the natural history of freshwater lake bacteria. **Microbiology and Molecular Biology Reviews**. doi: 10.1128/MMBR.00028-10
7. Sharma, S et al. 2019. Widespread loss of lake ice around the Northern Hemisphere in a warming world. **Nature Climate Change**. doi: 10.1038/s41558-018-0393-5
8. Walsh, JR et al. 2016. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. **PNAS**. doi: 10.1073/pnas.1600366113
9. Watras, CJ et al. 2014. Decadal oscillation of lakes and aquifers in the upper Great Lakes region of North America: hydroclimatic implications. **Geophysical Research Letters**. doi: 10.1002/2013GL058679
10. Winslow, LA et al. 2015. Small lakes show muted climate change signal in deep-water temperatures. **Geophysical Research Letters**. doi: 10.1002/2014GL062325



Niwot Ridge LTER

The entire study site of Niwot Ridge LTER (NWT) lies above 3,000 m elevation, approximately 35 km west of Boulder, Colorado. The NWT LTER program is built on a foundation of long term monitoring and experimental research designed to understand ecological dynamics of high elevation, mountain ecosystems, and their responsiveness to climate change. The program's overarching goals are to better understand where and when climate change leads to ecological change, to elucidate the mechanisms driving ecological sensitivity and buffering in this system, and to use this information to enhance forecasting, management, and conservation in mountain areas.



Between 2008-2018: **45** investigators

10 institutions represented

52 graduate students



Tundra

Principal Investigator:
Katharine Suding
University of Colorado, Boulder

Est. 1980
Funding Cycle:
LTER VII

NSF Program:
Biological Sciences /
Division of Environmental
Biology



Key Findings

Permafrost and stored ice are thawing.

Longer, warmer summers are associated with permafrost and stored ice thawing. The Arikaree Glacier is losing large volumes of ice and is expected to disappear in the next two decades. Thawing contributes to increased solute export associated with rock glaciers [Product 1] and winter carbon loss associated with tundra solifluction lobes [2].

Snow redistribution and snow melt timing are key to ecological response.

Longer, warmer summers increase heterogeneity in catchment snowmelt timing and flushing [3]. As snow melt flows through soils, it accelerates biogeochemical process rates in some areas [4], increasing tundra production. In windblown areas that receive little snow melt, however, the extended period of water limitation driven by these same climate conditions causes a decline in primary production [5].

Little treeline advance, increased tree mortality.

Treeline projections often focus on warming. However, NWT LTER researchers found that late summer water limitation may be a

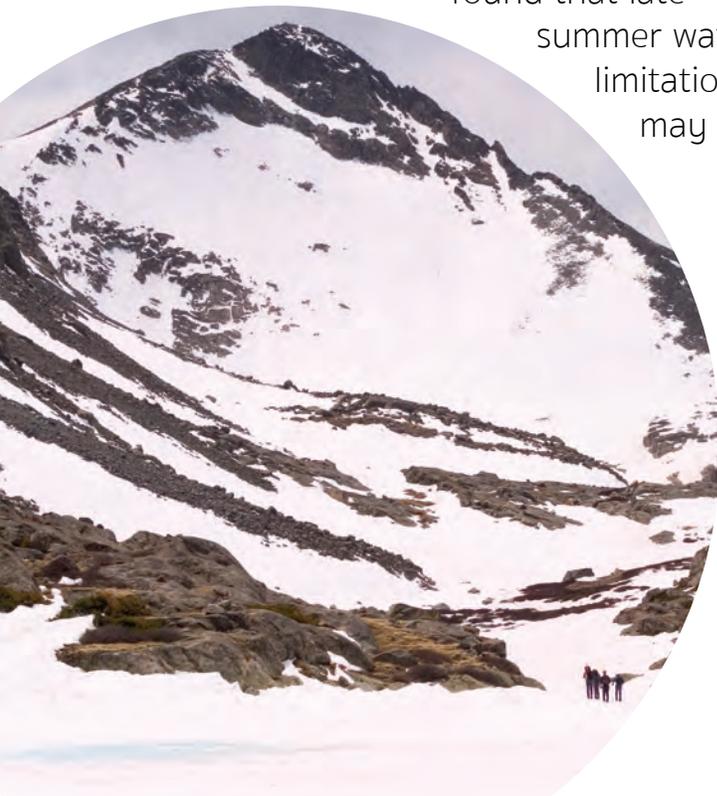
primary constraint on treeline expansion [6]. Longer, warmer summers also accelerate tree mortality, reduce tree recruitment, and decrease forest production within the subalpine forest [7].

Uphill spread of tundra vegetation. Once limited by a short growing season, vascular plants have colonized almost one fifth of the very high elevation unvegetated talus areas over the last four decades [6]. Diverse and active microbial communities may be key players in these colonization dynamics [8].

Decline of pikas. Pikas are widely considered a sentinel species for detecting ecological effects of climate change. Populations at Niwot Ridge and across the Western U.S. are projected to continue declining, and as a result, pikas have been considered for listing as threatened at the state and federal levels. Research at NWT LTER has shown that pikas in warming sub-surface areas show signs of chronic stress. [9]

Extended summer responses in lakes.

Climate driven changes in alpine lakes, such as earlier ice-off and warmer surface water temperatures, are associated with reduced summer streamflow, increased water column thermal stratification, and higher late summer solute (including nitrate) concentrations. [10]





Synthesis

The role of synchrony in ecological stability. This project led by two NWT LTER investigators uses statistical techniques to examine long term, spatially replicated data from both terrestrial and aquatic LTER sites to understand the timescales at which synchrony occurs, identify drivers of synchrony, and integrate the effects of population and community synchrony on ecological stability.

Synthesizing multi-scale observations, manipulations and models of soil organic matter.

Will Wieder, a NWT LTER investigator, leads this project combining soil organic matter data across LTER sites, Critical Zone Observatory (CZO) sites, the Detrital Input and Removal Treatments (DIRT) Network, and the Nutrient Network (NutNet). The goal is to evaluate theories of soil organic matter stabilization and understand the impact of experimental manipulations on soil organic matter across a variety of sites.

Partnerships

The Boulder Creek Critical Zone Observatory (CZO) | NEON | NOAA | National Atmospheric Deposition Program (NADP) | AmeriFlux | City of Boulder

Data Accessibility

Long term climate records in the NWT data archive include continuous measurements from stations established in the 1950s. The local data catalog is linked to the Environmental Data Initiative (EDI) repository through the PASTA API. This recently implemented solution improves NWT LTER's ability to version data, track updates, and more rapidly deliver datasets to EDI.

Photo credits: Erika Zambello (top); NWT LTER (right)



Broader Impacts

Graduate seminar in communication. Graduate students learn strategies for avoiding jargon, assessing prior knowledge, and engaging public audiences in meaningful scientific conversations. Students in the seminar share NWT LTER science with public audiences by teaching early elementary school children, developing short online videos, giving lectures to volunteer naturalist groups, leading tours of the research sites, and attending *Meet a Scientist* events at the public library.

Sharing alpine science. New partnerships with Winter Wildlands Snow School, Wild Bear Ecology Center Nature Camp, Nature Kids Lafayette, and the Colorado University

Museum of Natural History have allowed NWT LTER researchers to share their science with over 300 students during 2019. The NWT LTER Schoolyard Book, *My Water Comes from the Mountains*, was used for outreach, along with a new curriculum and materials kit, in Boulder Valley School District (~80 fourth grade classrooms) and in 15 other communities around the state.

Engaging city staff and residents. A climate change seminar and a monthly newsletter are used to communicate NWT LTER research and high level findings to City of Boulder staff as a “Monthly Water Quality Update.”



Top Products

Photo credits: William Bowman (above and cover)

1. Barnes, RT et al. 2014. Thawing glacial and permafrost features contribute to nitrogen export from Green Lakes Valley, Colorado Front Range, USA. **Biogeochemistry**. doi: 10.1007/s10533-013-9886-5
2. Knowles, JF et al. 2019. Evidence for non-steady state carbon emissions from snow-scoured alpine tundra. **Nature Communications**. doi: 10.1038/s41467-019-09149-2
3. Jepsen, SM et al. 2012. Interannual variability of snowmelt in the Sierra Nevada and Rocky Mountains, United States: Examples from two alpine watersheds. **Water Resources Research**. doi: 10.1029/2011WR011006
4. Darrouzet-Nardi, A et al. 2011. Hot spots of inorganic nitrogen availability in an alpine-subalpine ecosystem, Colorado Front Range. **Ecosystems**. doi: 10.1007/s10021-011-9450-x
5. Wieder, WR et al. 2017. Ecosystem function in complex mountain terrain: combining models and long-term observations to advance process-based understanding. **Journal of Geophysical Research: Biogeosciences**. doi: 10.1002/2016JG003704
6. Bueno de Mesquita, CP et al. 2017. Topographic heterogeneity explains patterns of vegetation response to climate change (1972–2008) across a mountain landscape, Niwot Ridge, Colorado. **Arctic, Antarctic and Alpine Research**. doi: 10.1080/15230430.2018.1504492
7. Andrus, RA et al. 2018. Moisture availability limits subalpine tree establishment. **Ecology**. doi: 10.1002/ecy.2134
8. King, AJ et al. 2010. Biogeography and habitat modelling of high-alpine bacteria. **Nature Communications**. doi: 10.1038/ncomms1055
9. Wilkening, JL et al. 2015. Relating sub-surface ice features to physiological stress in a climate sensitive mammal, the American pika (*Ochotona princeps*). **PLOS one**. doi: 10.1371/journal.pone.0119327
10. Preston, DL et al. 2016. Climate regulates alpine lake ice cover phenology and aquatic ecosystem structure. **Geophysical Research Letters**. doi: 10.1002/2016GL069036



Palmer Station Antarctica LTER

The Palmer Antarctic (PAL) LTER program pursues a comprehensive understanding of the seasonal sea ice-influenced ecosystem south of the Antarctic Polar Front, including climate, plants, microbes, animals, biogeochemical processes, ocean, and sea ice. Since its establishment in 1990, the PAL LTER's central hypothesis has been that the seasonal and interannual variability of sea ice affects all levels of the Antarctic marine ecosystem, from the timing and magnitude of primary production to the breeding success and survival of penguins and whales. The site's location on the western side of the Antarctic peninsula (WAP) addresses multiple spatial and temporal scales. The goal of PAL LTER is to understand how long term change drives food web and biogeochemical dynamics in a region where the marine system is transitioning from polar to a subpolar.



Between 2008-2018:

17 investigators

11 institutions represented

48 graduate students



Marine

Principal Investigator:

Hugh Ducklow

Columbia University

Est. 1990

Funding Cycle:

LTER V

NSF Program:

Biological Sciences /
Division of Environmental
Biology



Key Findings

Keystone species ranges are changing.

Shifts in sea ice are affecting the WAP ecosystem and biogeochemistry [Products 1, 2]. Despite dramatic shifts in Antarctic food webs [3, 4], the number of the keystone krill species (*Euphausia superba*) has not changed significantly over the PAL LTER study area [5]. However, researchers have observed reduced juvenile recruitment following positive anomalies of the Southern Annular Mode [6]. North of PAL LTER, *E. superba* population centers in the southwest Atlantic sector have been contracting southward for the past 90 years.

Ecosystem resilience. Between 2010 and 2017, the PAL LTER study area experienced cooler winter air temperatures, cooler summer surface ocean temperatures, and longer ice seasons relative to the first

decade of the 21st century (but not relative to the 1950s-1970s). This has slowed sea ice declines, which is associated with increased primary

productivity and ocean CO₂ drawdown [7, 8]. Springtime phytoplankton productivity and krill recruitment increased in years with high winter sea ice, which fed directly into penguin diets [6]. These processes are allowing researchers to assess the potential for food web recovery [1].

High trophic levels respond to West Antarctic Peninsula warming. Rapid warming in the WAP coincides with increases in gentoo penguin and decreases in Adélie penguin populations. While foraging ranges of Adélies and gentoos overlap with each other and with krill density maxima near Palmer Station, the vertical grazing ranges of the two penguin species differ [9]. This

suggests that declines in Adélie penguin populations along the WAP are more likely due to direct (snowfall) and indirect (food web alterations) climate impacts on their life histories, rather than direct competition for food [10].

Do whales and penguins compete? Humpback whale populations are growing at their biological maximum as they recover from intense commercial whaling. New cetacean research at PAL LTER shows that humpbacks forage in close proximity to the penguins near Palmer Station, and in similar portions of the water column used by Adélie penguins during critical chick rearing periods [9]. Palmer LTER researchers plan to quantitatively assess whether this observation is an indication of competition between baleen whales and penguins.

Climate forcing of the West Antarctic Peninsula. Over the past five decades, the West Antarctic Peninsula (WAP) has experienced changes related to rapidly warming winter atmospheric temperatures, dramatic sea ice declines, and accelerated glacial melting. Interactions between ocean and atmospheric climate cycles (El Niño, Southern Annular Mode) influence shoreward heat delivery associated with deep warm ocean waters and alter the upper mixed ocean layer, productivity at the base of the food web, and carbon cycling on the continental shelves. [1, 4, 7]





Synthesis

Cross-site synthesis project with McMurdo Dry Valleys (MCM) LTER. In 2016, three joint papers in *BioScience* identified common ecological responses to physical forcing in PAL and MCM LTER, two highly disparate Antarctic ecosystems.

Coordinated sampling with colleagues in the British Antarctic Survey. Joint and coordinated sampling since the mid-1990s has resulted in complementary time series sampling at Palmer and Rothera stations and regional sampling along the WAP. Palmer LTER researchers helped organize an international workshop in 2018 that resulted in a special issue of *Philosophical Transactions of the Royal Society* that focused on WAP physical, chemical, and biological dynamics.



Data Accessibility

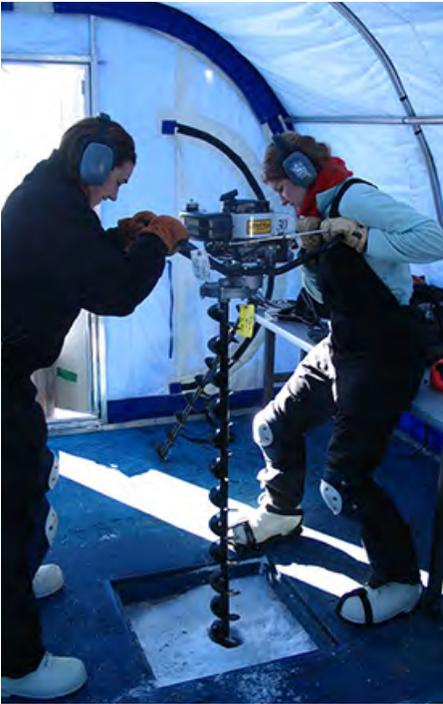
All Palmer Station and WAP data collected over the past 26 years is maintained in the PAL LTER data archive and posted to the Environmental Data Initiative (EDI) repository, regardless of the funding source. Easy access to these datasets has proven invaluable, especially for collaborations and synthesis studies.

Partnerships

NSF Office of Polar Programs | NOAA | NASA | Gordon & Betty Moore Foundation | G. Unger Vetelsen Foundation



Broader Impacts



Professional development for teachers. Almost 7,000 middle and high school students participated in a year-long program with the PAL LTER. Seventy-five educators participated in a week-long professional development program (Sci-I) that focused on incorporating PAL LTER data into teaching. The Sci-I program culminated in a student research symposium at Rutgers University.

Classroom video calls. Palmer LTER scientists and graduate students worked with the education and outreach team to offer live video teleconference calls (VTCs) between Palmer Station and U.S. classrooms. During the 2017 field season, for example, PAL LTER reached 23 educators and approximately 1,725 students from 5 states (NY, NJ, CA, NC, MA) in grades 5-12.

You're the Expert Podcast. National Public Radio (NPR) shared PAL LTER research stories on their *You're the Expert* program. Approximately 300 students, faculty, and staff from Rutgers University attended the taping of the show and NPR reports 250,000 downloads to date.

Palmer Station at the movies. With NSF support, the PAL LTER team produced a full length documentary on Palmer Station research entitled *Antarctic Edge: 70 Degrees South*. Undergraduate music and art students from Rutgers University collaborated with researchers to edit and develop a musical score for the film, which was broadcast at theaters across the U.S. and was available for download on iTunes.



Top Products

1. Schofield, O et al. 2018. Changes in upper ocean mixed layer and phytoplankton productivity along the West Antarctic Peninsula. **Philosophical Transactions of the Royal Society**. doi 10.1098/rsta.2017.0173
2. Bowman, JS et al. 2018. Recurrent seascape units identify key ecological processes along the western Antarctic Peninsula. **Global Change Biology**. doi: 10.1111/gcb.14161
3. Montes-Hugo, M et al. 2009. Recent changes in phytoplankton communities associated with rapid regional climate change along the Western Antarctic Peninsula. **Science**. doi: 10.1126/science.1164533
4. Sailley, S et al. 2013. Carbon fluxes and pelagic ecosystem dynamics around the West Antarctic Peninsula Adélie penguin colonies: An inverse model analysis. **Marine Ecology Progress Series**. doi: 10.3354/MEPS10534
5. Steinberg, DM et al. 2015. Long-term (1993-2013) changes in macrozooplankton off the Western Antarctic Peninsula. **Deep Sea Research II**. doi: 10.1016/j.dsr.2015.02.009
6. Saba, GK et al. 2014. Winter and spring controls on the summer food web of the coastal West Antarctic Peninsula. **Nature Communications**. doi: 10.1038/ncomms5318
7. Brown, MS et al. 2019. Enhanced oceanic CO₂ uptake along the rapidly changing West Antarctic Peninsula. **Nature Climate Change**. doi: 10.1038/s41558-019-0552-3
8. Stukel, MR. et al. 2015. The Imbalance of New and Export Production in the Western Antarctic Peninsula, a Potentially "Leaky" Ecosystem. **Global Biogeochemical Cycles**. doi: 10.1002/2015GB005211
9. Cimino, MA et al. 2016. Climate-driven sympatry may not lead to foraging competition between congeneric top-predators. **Scientific Reports**. doi: 10.1038/srep18820
10. Cimino, MA et al. 2019. The interaction between island geomorphology and environmental parameters drives Adélie penguin breeding phenology on neighboring islands near Palmer Station, Antarctica. **Ecology and Evolution**. doi: 10.1002/ece3.5481

Photo credits: PAL LTER & U.S. LTER



Plum Island Ecosystems LTER

Photo credit: JS Aber, SW Aber, & V Valentine

The Plum Island Ecosystems (PIE) LTER site is a linked watershed-marsh-estuarine system located north of Boston, Massachusetts. The brackish and saline tidal wetlands of the PIE LTER form the major portion of the “Great Marsh,” the largest contiguous intact marsh on the northeastern coast of the United States. Over 550 km² of upland are drained by three rivers. The PIE LTER works towards understanding how land-marsh-estuary-ocean ecosystems respond to changes in three key drivers over the long term: climate, sea level, and human activities.



Between 2008-2018:

46 investigators

29 institutions represented

107 graduate students



Coastal

Principal Investigator:

Anne Giblin

Marine Biological
Laboratory

Est. 1998

Funding Cycle:
LTER IV

NSF Programs:

Geoscience / Division of
Ocean Sciences
Biological Sciences / Division
of Environmental Biology



Key Findings

Sea-level rise and storms are altering salt marshes. For marshes where rates of sea level rise exceed about 3 mm/year, external sediment supply is critical to marsh survival. Although riverine sediment inputs to the Great Marsh are low, PIE LTER research has shown that marsh edge erosion during moderate intensity storms currently supplies enough sediment to maintain the marsh platform. However, with accelerating sea level rise, this will not be the case. Landscape scale studies of spatial and temporal changes (rather than relying on point measurements of platform accretion) provide more reliable information and allow better predictions to be made about future changes. Plum Island LTER is developing GIS methods to make more statistically robust comparisons between historical and current maps. [Products 1-4]

Consumers respond unexpectedly to nutrient enrichment. For the first six years of an ongoing 13-year nitrate addition experiment in tidal creeks, benthic algae, invertebrate prey, and a small fish, the mummichog, showed a classic positive bottom-up response to added nutrients. However, after six years, creek

banks began to collapse and mummichog abundance in fertilized creeks declined relative to reference sites, likely because the changing shape of creek channels cut off access

to food resources on the marsh platform. Amphipods in fertilized creeks also developed a much higher incidence of trematode parasites, which made them more vulnerable to predation. [5, 6]

Microbial dormancy and diversity. A decade of nutrient enrichment significantly increased rates of oxygen uptake and nitrate reduction in sediment. Surprisingly, the proportion of the dormant microbial population increased (overall composition of the microbial community remained unchanged). This response to a perturbation may reflect the microbial community's strategy for maintaining diversity in a highly dynamic environment. [7, 8]

Controls on nitrogen fluxes to estuaries. Despite expanded suburban development, nitrogen fluxes to the estuary have remained steady since the early 1990s. Riverflow, which is becoming more variable along with climate, largely determines nitrogen retention. Imbalances between nutrient supply and demand reduce nutrient regulation during higher flows. Work at PIE LTER helped lead to a generalized framework for modeling material fluxes at river network scales – the River Network Saturation framework. Knowing when and where river networks become saturated for different constituents allows scientists and managers to better extrapolate to broader spatial scales, clarify the role of rivers in continental element cycles, and identify policy priorities. [9, 10]

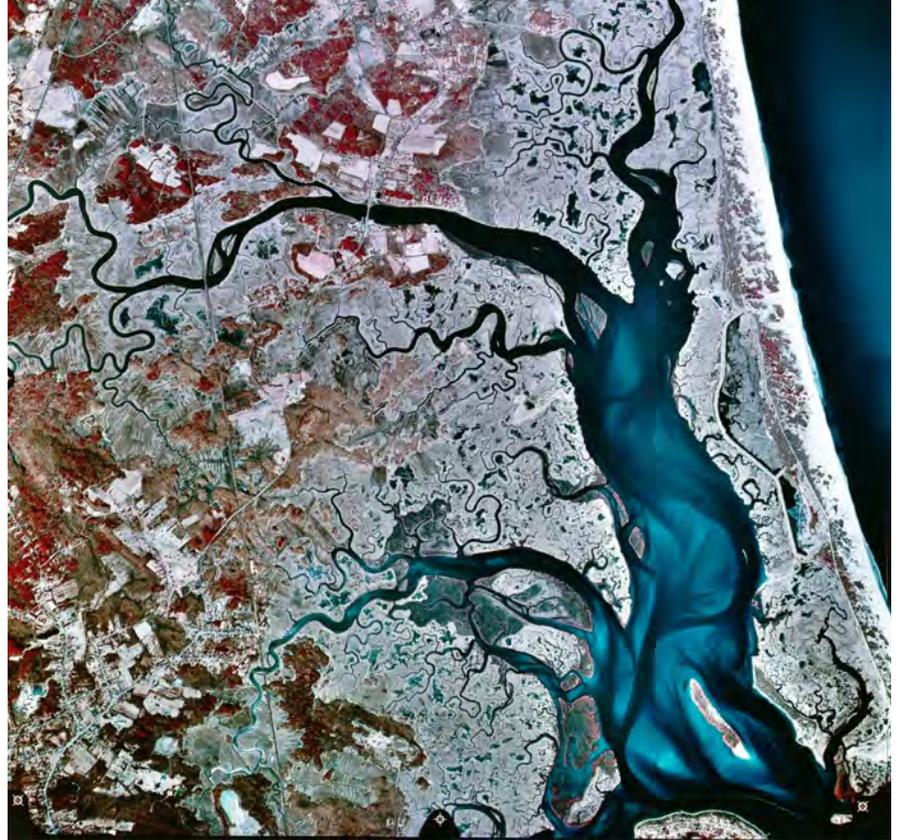


Synthesis

Re-examining nitrogen cycling in coastal ecosystems. Until recently, it was thought that assimilation and nitrogen (N) loss through denitrification were the two major fates of nitrate entering coastal ecosystems. However, a PIE LTER-led synthesis study of 55 coastal sites demonstrated that dissimilatory nitrate reduction to ammonium, an N-conserving process, is more critical than previously believed, and sometimes the dominant nitrate reduction process in coastal wetlands (Giblin et al., 2013).

Evaluating the importance of “blue” carbon. Coastal vegetated wetlands have recently been identified as important global carbon sinks. They are also highly vulnerable to direct degradation by human activity. This review estimated how the magnitude of this sink may be changing with global warming, sea-level rise, agricultural expansion, and other stresses (Hopkinson et al., 2012).

Coastal sustainability. Along with VCR and GCE LTER, PIE LTER has Coastal SEES funding focusing on how vulnerable or sustainable tidal wetlands are to climate-driven change. The project articulates feedbacks between tidal wetlands and adaptation of coastal communities.



Data Accessibility

Plum Island LTER has maintained online, offline, and offsite backups of site datasets since the mid-1990s. Dataset entry, quality checks, and updates to the website are followed by corresponding updates to the Environmental Data Initiative (EDI) repository. High quality data and PIE LTER’s open data policy makes information easily accessible to collaborators. As an NSF-OCE funded LTER site, PIE data are also available through the Biological & Chemical Oceanography Data Management Office, BCO-DMO.

Partnerships

Ameriflux | Mass Audubon | Parker River Fish & Wildlife Refuge | Essex County Greenbelt | Marine Biological Laboratory





Broader Impacts

K-12 education. The PIE LTER K-12 Schoolyard program, co-led by Mass Audubon, provides experiential learning opportunities to approximately 1,000 students and 50 teachers annually across 10 schools (grades 5-12). A new project has a climate change focus, which includes the use of vegetation transects measured by program participants for the past 25 years.

Professional development and outreach. As part of a summer professional development course for teachers, Mass Audubon educators and PIE LTER researchers collaborate with teachers to produce “[Data Nuggets](#)” and lesson plans based on real data. PIE LTER researchers also help teachers develop community based environmental stewardship projects with the Gulf of Maine Institute.



Science journalists in the field. Each year 6-8 journalists participate in the 12-day hands-on Logan Science Journalism program on coastal eutrophication for mid-career journalists.

Mentoring graduate and undergraduate students. Each summer 10-14 undergraduate and graduate students work and live at the PIE LTER field house. Many others commute almost daily from nearby colleges and universities.

Top Products

1. Morris, JT et al. 2013. Salt marsh primary production and its responses to relative sea level and nutrients in estuaries at Plum Island, Massachusetts, and North Inlet, South Carolina, USA. **Oceanography**. doi: 10.5670/oceanog.2013.48
2. Leonardi, N et al. 2016. A linear relationship between wave power and erosion determines salt-marsh resilience to violent storms and hurricanes. **PNAS**. doi: 10.1073/pnas.1510095112
3. Hopkinson, CS et al. 2018. Lateral Marsh Edgy Erosion as a Source of Sediments for Vertical Marsh Accretion. **J. Geophysical Research, Biogeosciences**. doi: 10.1029/2017JG004358
4. Pontius Jr., RG. and M. Millones. 2011. Death to Kappa: birth of quantity disagreement and allocation disagreement for accuracy assessment. **International Journal of Remote Sensing**. doi: 10.1080/01431161.2011.552923
5. Deegan LA et al. 2012. Coastal eutrophication as a driver of salt marsh loss. **Nature**. doi: 10.1038/nature11533
6. Johnson, DS et al. 2009. Large-scale manipulations reveal top-down and bottom-up controls interact to alter habitat utilization by saltmarsh fauna. **Marine Ecology Progress Series**. doi: 10.3354/meps07849
7. Kearns, PJ et al. 2016. Nutrient enrichment induces dormancy and decreases diversity of active bacteria in salt marsh sediments. **Nature Communications**. doi: 10.1038/ncomms12881
8. Koop-Jakobsen, K and AE Giblin. 2010. The effect of increased nitrate loading on nitrate reduction via denitrification and DNRA in salt marsh sediments. **Limnol. Oceanogr.** doi: 10.4319/lo.2010.55.2.0789
9. Morse, NB and WM Wollheim. 2014. Climate variability masks the impacts of land use change on nutrient export in a suburbanizing watershed. **Biogeochemistry**. doi: 10.1007/s10533-014-9998-6
10. Wollheim WM et al. 2018. River network saturation concept: factors influencing the balance of biogeochemical supply and demand of river networks. **Biogeochemistry**. doi: 10.1007/s10533-018-0488-0



Santa Barbara Coastal LTER

Photo credit: U.S. LTER

Santa Barbara Coastal (SBC) LTER focuses on giant kelp forests fringing the coast of the Santa Barbara Channel in semiarid southern California. Kelp forests are prominent on shallow reefs at the coastal margin in temperate regions of the world and are highly valued for their ecosystem goods and services. Research at SBC LTER is dedicated to understanding how oceanic and terrestrial processes alter material flows to influence the ecology of these iconic coastal systems. In its first 19 years, SBC LTER has demonstrated the surprising resilience of giant kelp forests in the face of natural and human disturbance and the key role of dispersal and connectivity in driving that resilience. Through the combination of sustained measurements, long term experiments, satellite imagery, and modeling, SBC LTER is developing a mechanistic understanding of ecosystem structure and function and is poised to predict the impacts of climate change and human activities on kelp forest ecosystems.



Between 2008-2018:

68 investigators

16 institutions represented

101 graduate students



Coastal

Principal Investigator:
Robert Miller
Marine Science Institute,
University of California, Santa
Barbara

Est. 2000
Funding Cycle:
LTER IV

NSF Program:
Geosciences / Division of
Ocean Sciences
Biological Sciences / Division
of Environmental Biology



Key Findings

Giant kelp shapes an entire ecosystem.

Results from long term measurements and experiments reveal that climate-driven disturbances that alter giant kelp abundance cascade through the kelp forest community, affecting biodiversity and ecosystem function. These effects are due to kelp's overwhelming influence on environmental conditions and habitat availability rather than its effects as a food source for fauna. [Products 1, 2]

Fires mobilize nutrients to the ocean. Fire and land use affect the amount and timing of nutrient organic matter and sediment delivery from watersheds to the ocean. Drought and fire followed by rain causes large fluxes of terrestrial nutrients to the coastal ocean. During storms, runoff plumes containing high concentrations of nutrients remain close to the coast, but are advected offshore and quickly diluted once the storms pass, thereby reducing the contribution of land-derived nutrients to the productivity of coastal ecosystems. [3, 4]



Phytoplankton are the breadbasket of the kelp forest. Decades of

research based on carbon stable isotope analyses supported the idea that macroalgal detritus, especially that of kelp, is a major source of food to coastal marine ecosystems, particularly suspension feeders. Comparative and experimental research from SBC LTER has overturned this paradigm, showing that phytoplankton, not kelp, are the main food resource for coastal benthic suspension feeders. [5, 6]

Kelp forests are surprisingly resilient to unprecedented warming. A marine heat wave of extreme magnitude and duration in 2014-15 allowed SBC LTER researchers to test predictions about the effects of climate change on kelp forests. Although kelp was diminished by the prolonged high temperature and low nitrate conditions, it rebounded quickly, and most other flora and fauna were not greatly affected. Ocean sampling revealed that ammonium and urea persisted during warm periods and experiments showed that kelp can use these recycled nitrogen sources. [7-8]





Photo credit: Erika Zambello / U.S. LTER

Synthesis

Big waves trump grazing and nutrients. Cycles of disturbance and recovery in kelp forests occur on time scales of years, making it an ideal system for studying processes that play out over much longer time scales in many ecosystems. Cross-site research between SBC LTER and researchers from central California demonstrated that regional differences in wave disturbance overwhelmed those in nutrient supply and grazing intensity to determine differences in giant kelp standing biomass and primary production. [9]

Diverse ecosystems undergo drastic change. Abrupt transitions or regime shifts are increasing for many ecosystems. Santa Barbara Coastal LTER contributed to a cross-site study of ecological responses to a changing environment in pelagic ocean, coastal benthic, polar marine, and semi-arid grassland ecosystems. In the majority of cases, abrupt transitions and underlying mechanisms were detected, providing information to help manage state changes. [10]

Partnerships

Santa Barbara Channel Marine Biodiversity Observation Network (MBON) | NASA | Bureau of Ocean Energy Management | University of California, Santa Barbara

Data Accessibility

The SBC LTER's information management system focuses on ease of data access, organization, integrity, and long term preservation. A flexible framework is designed to adapt to changes in NSF and community guidelines as information needs evolve. Since its inception, SBC has been a leader in the LTER Network Information System, working with other LTER sites and the wider community, including the National Center for Ecological Analysis and Synthesis, to improve data integration and availability within and beyond the LTER Network. In keeping with this history, SBC LTER is playing a key role in the new Ecological Data Initiative to curate LTER data network-wide.

Photo credit: Erika Zambello / U.S. LTER



Broader Impacts

Hands on science for girls. Tech Trek is an on-campus residential science and math summer program at UC Santa Barbara to develop interest and self confidence in female students starting eighth grade, using hands-on field, laboratory and classroom activities designed around SBC LTER research.

Local impacts of global change.

Collaborating with scientists from Scripps Institution of Oceanography and the U.S. Geological Survey, SBC LTER investigators forecasted the vulnerability of Santa Barbara County's wetlands, watersheds and beaches to sea level rise. The results were presented in public meetings, and will be used by local land use planners and decision makers to inform coastal land use and sea level rise adaptation plans.



Photo credit: Erika Zambello / U.S. LTER

Teaching the teachers. Four LTER sites, including SBC LTER, founded the groundbreaking Math Science Partnership project: *Pathways to Environmental Literacy* to connect research with teacher professional development. Site researchers and educators continue to deliver research based curricula

on key concepts, including ocean circulation, weather, and biodiversity, to over 1,000 middle and high school students per year.

The Golden Forest.

The new SBC LTER book in the LTER Schoolyard Series presents coastal ecology in a beautifully illustrated format. Owen visits

his cousin Neko in California, where they have a snorkeling adventure and learn about kelp's role in the water and on coastal beaches.

Top Products

1. Byrnes, JE et al. 2011. Climate-driven increases in storm frequency simplify kelp forest food webs. **Global Change Biology**. doi: 10.1111/j.1365-2486.2011.02409.x
2. Miller, RJ et al. 2018. Giant kelp, *Macrocystis pyrifera*, increases faunal diversity through physical engineering. **Proceedings of the Royal Society B: Biological Sciences**. doi: 10.1098/rspb.2017.2571
3. Romero, L et al. 2016. Characterizing storm water dispersion and dilution from small coastal streams. **Journal of Geophysical Research**. doi: 10.1002/2015JC011323
4. Aguilera, R and Melack, JM. 2018. Relationships among nutrient and sediment fluxes, hydrological variability, fire, and land cover in coastal California catchments. **Journal of Geophysical Research**. doi: 10.1029/2017JG004119
5. Page, HM et al. 2008. Assessing the importance of land and marine sources of organic matter to kelp forest food webs. **Marine Ecology Progress Series**. doi: 10.3354/meps07382
6. Miller, RJ et al. 2013. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of particulate organic matter in the Santa Barbara Channel: drivers and implications for trophic inference. **Marine Ecology Progress Series**. doi: 10.3354/meps10098
7. Reed, DC et al. 2016. Extreme warming challenges sentinel status of kelp forests as indicators of climate change. **Nature Communications**. doi: 10.1038/ncomms13757
8. Smith, JM et al. 2018. Urea as a source of nitrogen to giant kelp (*Macrocystis pyrifera*). **Limnology and Oceanography Letters**. doi: 10.1002/lol2.10088
9. Reed, DC et al. 2011. Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. **Ecology**. doi: 10.1890/11-0377.1
10. Bestelmeyer, BT et al. 2011. Analysis of abrupt transitions in ecological systems. **Ecosphere**. doi: 10.1890/ES11-00216.1



Sevilleta LTER

Arid and semi-arid ecosystems cover more than 40% of Earth's land surface and are expanding in extent. Due to their fluctuating nature, drylands are excellent settings to investigate the ecological consequences of environmental variability. The Sevilleta (SEV) LTER site represents the convergence of six major North American dryland ecosystems – pinon-juniper woodlands, juniper savannas, riparian cottonwood forests, plains grasslands, and Chihuahuan Desert grasslands and shrublands. Combined, these ecosystems create a powerful opportunity to test how ecosystem structure and function respond to environmental variability and change.

The SEV LTER program spans 30 years of long term data, experiments, specimen archives, and theory. Sevilleta LTER researchers are developing new theories to predict the consequences of environmental variability over space, time, and biological scales and generating the long term data needed to test these predictions. Current research is focused on the question: How do long term trends in climate variability drive the dynamics of dryland ecosystems and transitions among them?



Between 2008-2018:

73 investigators

33 institutions represented

48 graduate students



Mixed Landscape

Principal Investigator:
Jennifer Rudgers
University of New Mexico

Est. 1989
Funding Cycle:
LTER VI

NSF Program:
Biological Sciences
/ Division of
Environmental Biology



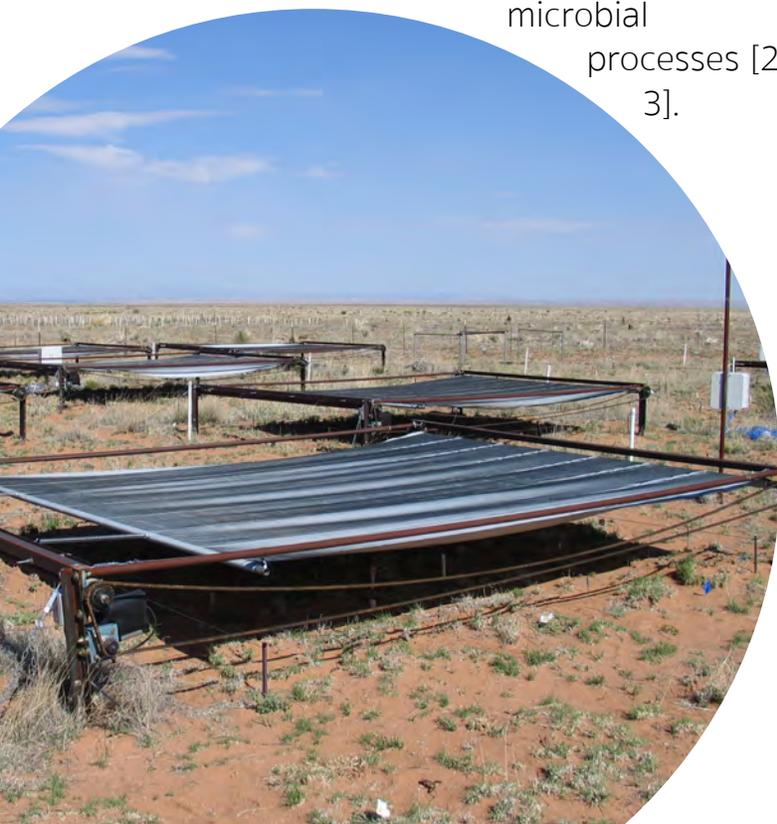
Key Findings

Climate variability interacts with average weather conditions. The climate of SEV LTER ecosystems has become drier and more variable during the past 100 years. SEV LTER research is gaining new insight into the biological consequences of these dual climate changes. For instance, increased climate variability has benefitted desert grassland during dry periods but reduced its productivity in wet periods, while plains grassland has been more sensitive to variability during droughts. [Product 1].

Challenging the pulse-reserve paradigm. Pulse-reserve theory has been a dominant conceptual framework for drylands since the 1970s. Detailed long term observations and experiments at the SEV LTER revealed that individual rainfall pulses rarely produce significant reserves and that many ecosystem processes do not “pulse” on the same time scales. SEV LTER researchers have improved pulse-reserve theory with the Threshold Delay Nutrient Dynamics model, which incorporated microbial processes [2, 3].

Causes and consequences of ecosystem state transitions. Groundbreaking interdisciplinary work by SEV LTER researchers has documented biophysical feedbacks at ecosystem boundaries. Key differences in the mechanisms of drought tolerance explained the conversion of pinon woodlands into juniper savannas. Creosote bush promoted nighttime warming that can favor its seedling establishment at grassland-to-shrubland ecotones. State transitions have important consequences for ecosystem climate sensitivity and carbon sequestration. During the past decade, SEV biomes ranged from carbon (C) sources to the atmosphere (~ 400 g C m⁻², desert grassland) to sinks (~ 1500 g C m⁻², pinon-juniper woodland). [4-6]

Conceptual and empirical advances in desert microbial ecology. Researchers at SEV LTER led efforts to characterize fungi and bacteria in drylands and document their responses to environmental change. SEV LTER pioneered new assays of microbial function, including carbon use efficiency and ecoenzymatic stoichiometry. They quantified how microbes in roots maintain plant species coexistence and temporal stability in plant communities and how biological soil crusts affect community and ecosystem dynamics. [7]





Synthesis

Expanding the range. As one of the few dryland nodes in the Nutrient Network Project, SEV LTER extends the range of inference for understanding relationships among nutrients, biodiversity, and productivity. [8]

Streams and rivers retain nitrogen. SEV LTER researchers studied streams and rivers in central New Mexico as sinks for bioavailable nitrogen. Collaborative work established relationships among nitrate, denitrification, and ecosystem photosynthesis and respiration that are generalizable across biomes. [9]

Long term experiments to improve prediction. Synthesis of chronic resource manipulations at SEV LTER and elsewhere launched a novel, hierarchical conceptual framework for predicting the ecological consequences of global environmental change. [10]

Partnerships

Sevilleta National Wildlife Refuge | Los Alamos National Laboratory | Sandia National Laboratory | University of New Mexico (UNM) | UNM Sevilleta Field Station | UNM Civil, Construction and Environmental Engineering | New Mexico Museum of Natural History and Science | Bosque Ecosystem Monitoring Program

Photo credits: Will Pockman (top); Bosque Ecosystem Monitoring Program (bottom)

Data Accessibility

Sevilleta LTER information management provides high quality, well documented, easily accessible data through the Environmental Data Initiative, with 219 data packages. Partnership with the Museum of Southwestern Biology has established a DNA repository for monitoring long term evolutionary change. Ongoing projects are building new interfaces with genomic and museum databases as well as publicly accessible model and statistical code.



Broader Impacts

STEM workforce development. Sevilleta LTER recruits and trains a diverse STEM workforce through activities such as distributed graduate seminars and a data analysis course, course-based undergraduate research modules, collaborative teaching with the Southwestern Indian Polytechnic Institute, and an REU Site program.

Partnering with federal land managers. Sevilleta LTER partners with the Sevilleta National Wildlife Refuge, which receives 13,000 visitors per year. Collaboration with land managers occurs at local, regional, and national levels and informs prescribed fire, climate forecasts, disease outbreaks, and wildlife management.

Schoolyard data informs land and river management. Sevilleta LTER partners with the Bosque Ecosystem Monitoring Program (BEMP) to reach 9,000-10,000 participants each year (55% Hispanic, 11% Native American). Combining long term scientific research with educational outreach, BEMP engages K-12 students and their teachers in hands-on monitoring of the riparian forest (or bosque) of the Rio Grande. Data collected by K-12 and university students are used by federal and state agencies, including the U.S. Army Corps of Engineers, U.S. Fish and Wildlife Service, City of Albuquerque Open Space, and Mid Rio Grande Stormwater Quality Team to inform multimillion dollar management decisions.



Top Products

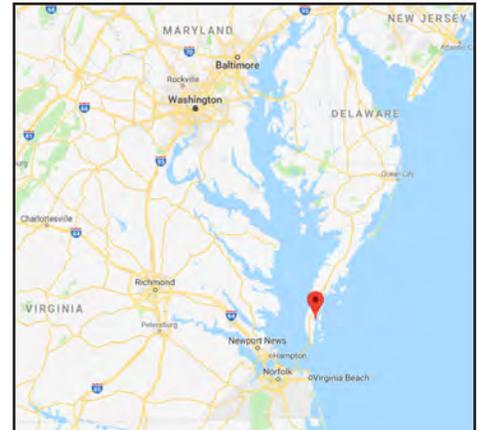
1. Rudgers, JA et al. 2018. Climate sensitivity functions and net primary production: A framework for incorporating climate mean and variability. **Ecology**. doi: 10.1002/ecy.2136
2. Thomey, ML et al. 2011. Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland. **Global Change Biology**. doi: 10.1111/j.1365-2486.2010.02363.x
3. Collins, SL et al. 2008. Pulse dynamics and microbial processes in arid ecosystems. **Journal of Ecology**. doi: 10.1111/j.1365-2745.2008.01362.x
4. McDowell, N et al. 2008. Mechanisms of plant survival and mortality during drought. **New Phytologist**. doi: 10.1111/j.1469-8137.2008.02436.x
5. Turnbull, L et al. 2008. A conceptual framework for understanding semi-arid land degradation: ecohydrological interactions across multiple-space and time scales. **Ecohydrology**. doi: 10.1002/eco.4
6. Anderson-Teixeira, KJ et al. 2011. Differential responses of production and respiration to temperature and moisture drive carbon balance across a climatic gradient in New Mexico. **Global Change Biology**. doi: 10.1111/j.1365-2486.2010.02269.x
7. Sinsabaugh, RL et al. 2008. Stoichiometry of soil enzyme activity at global scale. **Ecology Letters**. doi: 10.1111/j.1461-0248.2008.01245.x
8. Adler, PB et al. 2011. Productivity is a poor predictor of plant species richness. **Science**. doi:10.1126/science.1204498
9. Mulholland, PJ et al. 2008. Stream denitrification across biomes and its response to anthropogenic nitrate loading. **Nature**. doi:10.1038/nature06686
10. Smith, MD et al. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. **Ecology**. doi:10.1890/08-1815.1



Virginia Coast Reserve LTER

Photo credit: Erika Zambello / U.S. LTER

The Virginia Coast Reserve (VCR) LTER program is based in the vast and undeveloped Virginia Coast Reserve, a coastal barrier system comprised of intertidal marshes, shallow coastal bays, and barrier islands. Research at the site is dedicated to understanding how sea-level rise, storms, and temperature extremes cause ecosystem transitions, and how state change in one ecosystem can propagate across the landscape through coupled dynamics. Over its history, the program has advanced state change theory for ecosystems dominated by foundation species, including feedbacks that either maintain or facilitate transitions, and leading indicators of tipping points. Through integrated studies of ecological and physical processes that include long term observations, experimental data, and mechanistic models, VCR LTER researchers are global leaders in predicting the impacts of climate on coastal ecosystems. Addressing the complexity and interdependence of ecosystems on the landscape is a critical frontier in projecting long term responses and resilience to climate change.



Between 2008-2018:

42 investigators

22 institutions represented

135 graduate students



Coastal

Principal Investigator:
Karen McGlathery
University of Virginia

Est. 1987
Funding Cycle:
LTER VII

NSF Program:
Biological Sciences
/ Division of
Environmental Biology



Key Findings

Restoration returns 'blue carbon' stores.

A 20-year landscape-scale experiment at VCR LTER was the first to show the role of restoration in reestablishing carbon burial in seagrass meadows, which matches natural systems after a decade. Virginia Coast Reserve scientists authored the international protocol through Verified Carbon Standards for issuing seagrass restoration carbon offset credits on the voluntary market. Carbon stored in sediments and sequestered in seagrass biomass is vulnerable to marine heatwaves that are projected to increase. [Products 1-3]

Climate change shifts grasslands to

shrublands. Over the last 30 years, nearly half of the upland area on the barrier islands has changed from grassland to shrub thickets, similar to transitions observed in other drylands. For coastal systems, this transition is driven by regional climate (higher winter temperatures, lower precipitation) and shrub feedbacks on microclimate (warmer winter and cooler summer temperatures). Shrub thickets may reduce the ability of islands to build upward and migrate landward in response to sea-level rise and storms. [2,7]

Sea-level rise and storms can cause marsh loss.

Long term VCR LTER and comparative studies define a threshold sea-level rise rate beyond which marshes cannot keep pace and drown. An early warning indicator of this state change is an increase in recovery time following flooding disturbances. Storms cause marsh loss by erosion in proportion to wave energy at the marsh edge. Smaller, more frequent storms, not hurricanes, are responsible for most marsh erosion, and this can be reduced by adjacent oyster reefs and seagrass meadows that attenuate waves. [4-6]

Coastal change is accelerating. Historically, this undeveloped landscape has been a shifting mosaic; a new 30-year retrospective now shows directional change and accelerating ecosystem loss. Barrier island upland area has declined by a third, and island marsh loss due to storm overwash has increased, especially in the last decade. Feedbacks between vegetation and sediment transport determine barrier island dune shape, and this affects island migration and the long term resilience of islands to storms. [8-10]





Synthesis

International collaboration. Scientists from VCR LTER have led national and international collaborations, involving multiple LTER and non-LTER sites, on marsh vulnerability to sea-level rise and storms, carbon sequestration, and barrier island dynamics in response to climate drivers. These collaborations leverage the near pristine nature of the VCR landscape and inform strategies for nature based solutions to climate change in coastal systems globally. Two synthesis books have been edited by VCR LTER scientists on barrier island dynamics and ecogeomorphology of tidal marshes.

Novel technologies. Virginia Coast Reserve LTER scientists have pioneered two novel technologies and partner with national and international collaborators to disseminate their use. The aquatic eddy covariance method continuously measures benthic metabolism. High resolution in-situ techniques measure turbulent flow and mixing.

Partnerships

University of Virginia | NOAA | U.S. Geological Survey | U.S. Department of Agriculture | U.S. Fish and Wildlife Service | Department of the Interior | Office of Naval Research | Sea Grant | Virginia Game and Inland Fisheries | The Nature Conservancy | Nutrient Network (NutNet) | AmeriFlux

Photo credits: Gordon Campbell at Altitude Gallery (top); Michael Cornish (bottom)

Data Accessibility

The VCR provides over 230 datasets, 53 of which have a duration of 10 years or longer. Data are provided to the research community via the site data catalog, the Environmental Data Initiative repository, and DataONE. Datasets have been downloaded over 29,000 times since 2012. The VCR LTER has been an active participant in LTER-wide data initiatives, and led the creation of the LTER Controlled Vocabulary and code-generation services.



Broader Impacts

Science literacy for diverse K-12 students. Field and classroom experiences provided by VCR LTER reach every student in the region, all from majority-minority Title 1 schools, at least twice before graduation. Water quality monitoring, watershed exploration, and meaningful educational watershed experiences with regional partners parallel VCR LTER studies and train students in observation, data collection, and analysis.

Environmental humanities.

Combining arts and humanities with place-based ecology is a signature of the VCR LTER. The practice of observation provides a shared foundation for VCR LTER's long running Art and Ecology professional development program. In collaboration with the University of Virginia, VCR LTER is launching the Environmental Humanities Conservatory. Sonifying long term data brings together music, ethics, and science to establish a trans-disciplinary community focused on coastal change.



Photo credit: Erika Zambello

Coastal resilience decision support. The 30-year partnership between VCR and The Nature Conservancy (TNC) is a model for data-informed management and resilience planning. Together with TNC, VCR LTER has developed the open access Coastal Resilience Mapping Tool using VCR long term data and models. Staff and researchers from VCR LTER participate in implementing the University of Virginia-led Resilience Action Feasibility Tool to help Virginia localities improve resilience to flooding and other coastal storm hazards.

Teacher training.

Professional development workshops in coastal ecology, art and ecology, and oyster restoration provide teachers with place-based outdoor experiences, curriculum development, classroom resources, and sustained partnerships. Each year VCR LTER engages more than 50 teachers who reach about 8,000 students in the Mid-Atlantic region.

Top Products

1. McGlathery, KJ et al. 2012. Recovery trajectories during state change from bare sediment to eelgrass dominance. **Marine Ecology Progress Series**. doi: 10.3354/meps09574
2. Oreska, MPJ et al. 2017. Seagrass blue carbon accumulation at the meadow-scale. **PLOS One**. doi: 10.1371/journal.pone.0176630
3. Carr, JA et al. 2012. Stability and resilience of seagrass meadows to seasonal and interannual dynamics and environmental stress. **Journal of Geophysical Research**. doi:10.1029/2011JG001744
4. Kirwan ML et al. 2016. Overestimation of marsh vulnerability to sea level rise. **Nature Climate Change**. doi: 10.1038/NCLIMATE2909
5. van Belzen, JJ et al. 2017. Vegetation recovery in tidal marshes reveals critical slowing down under increased inundation. **Nature Communications**. doi: 10.1038/ncomms15811
6. Leonardi, NN et al. 2016. A linear relationship between wave power and erosion determines salt-marsh resilience to violent storms and hurricanes. **PNAS**. doi: 10.1073/pnas.1510095112
7. Huang, H et al. 2018. Non-linear shift from grassland to shrubland in temperate barrier islands. **Ecology**. doi: 10.1002/ecy.2383
8. McGlathery, KJ et al. 2013. Nonlinear dynamics and alternative stable states in shallow coastal systems. **Oceanography**. doi: 10.5670/oceanog.2013.66
9. Zinnert, JC et al. 2019. Connectivity in coastal systems: barrier island vegetation influences upland migration in a changing climate. **Global Change Biology**. doi: 10.1111/gcb.14635
10. Durán Vinent, O and LJ Moore. 2015. Barrier island bistability induced by biophysical interactions. **Nature Climate Change**. doi: 10.1038/nclimate2474

16 References

1. Kuebbing, S. E. *et al.* Long-term research in ecology and evolution: a survey of challenges and opportunities. *Ecol. Monogr.* **88**, 245–258 (2018).
2. National Science Foundation. LTER program solicitation 79-64. (1979).
3. *Quantifying FAIR: metadata improvement and guidance in the DataONE repository network.* (2019).
4. Collins, S. L. *et al.* An integrated conceptual framework for long-term social–ecological research. *Front. Ecol. Environ.* **9**, 351–357 (2011).
5. Dodds, W. K. *et al.* Surprises and Insights from Long-Term Aquatic Data Sets and Experiments. *BioScience* **62**, 709–721 (2012).
6. Baatz, R. *et al.* Steering operational synergies in terrestrial observation networks: opportunity for advancing Earth system dynamics modelling. *Earth Syst. Dyn.* **9**, 593–609 (2018).
7. Jones, C. N., Nelson, N. G. & Smith, L. L. Featured Collection Introduction: The Emerging Science of Aquatic System Connectivity I. *JAWRA J. Am. Water Resour. Assoc.* **55**, 287–293 (2019).
8. Richter, D. D. *et al.* Ideas and perspectives: Strengthening the biogeosciences in environmental research networks. *Biogeosciences* **15**, 4815–4832 (2018).
9. Weintraub, S. R. *et al.* Leveraging Environmental Research and Observation Networks to Advance Soil Carbon Science. *J. Geophys. Res. Biogeosciences* **124**, 1047–1055 (2019).
10. Hughes, B. B. *et al.* Long-Term Studies Contribute Disproportionately to Ecology and Policy. *BioScience* **67**, 271–281 (2017).
11. Melillo, J. M. *et al.* Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. *Science* **358**, 101–105 (2017).
12. Peters, D. P. C., Yao, J., Browning, D. & Rango, A. Mechanisms of grass response in grasslands and shrublands during dry or wet periods. *Oecologia* **174**, 1323–1334 (2014).
13. Collins, S. L. *et al.* A Multiscale, Hierarchical Model of Pulse Dynamics in Arid-Land Ecosystems. *Annu. Rev. Ecol. Evol. Syst.* **45**, 397–419 (2014).
14. Gherardi, L. A. & Sala, O. E. Enhanced precipitation variability decreases grass- and increases shrub-productivity. *Proc. Natl. Acad. Sci.* **112**, 12735–12740 (2015).
15. Petrie, M. D. *et al.* Regional grassland productivity responses to precipitation during multiyear above- and below-average rainfall periods. *Glob. Change Biol.* **24**, 1935–1951 (2018).
16. Redfield, A. C. *On the Proportions of Organic Derivatives in Sea Water and Their Relation to the Composition of Plankton.* (University Press of Liverpool, 1934).

17. Tansley, A. G. The Use and Abuse of Vegetational Concepts and Terms. *Ecology* **16**, 284–307 (1935).
18. Lindeman, R. L. The Trophic-Dynamic Aspect of Ecology. *Ecology* **23**, 399–417 (1942).
19. Vitousek, P. M. & Reiners, W. A. Ecosystem Succession and Nutrient Retention: A Hypothesis. *BioScience* **25**, 376–381 (1975).
20. MacArthur, R. H. *Geographical Ecology: Patterns in the Distribution of Species*. (Princeton University Press, 1984).
21. Titman, D. Ecological competition between algae: experimental confirmation of resource-based competition theory. *Science* **192**, 463–465 (1976).
22. Tilman, D. *Resource Competition and Community Structure*. (Princeton University Press, 1982).
23. Bloom, A. J., Chapin, F. S. & Mooney, H. A. Resource Limitation in Plants-An Economic Analogy. *Annu. Rev. Ecol. Syst.* **16**, 363–392 (1985).
24. Rastetter, E. B. & Shaver, G. R. A Model of Multiple-Element Limitation for Acclimating Vegetation. *Ecology* **73**, 1157–1174 (1992).
25. Carpenter, S. R. *et al.* Nonpoint Pollution of Surface Waters with Phosphorus and Nitrogen. *Ecol. Appl.* **8**, 559–568 (1998).
26. Vitousek, P. M. *et al.* Human Alteration of the Global Nitrogen Cycle: Sources and Consequences. *Ecol. Appl.* **7**, 737–750 (1997).
27. Galloway, J. N. *et al.* Transformation of the Nitrogen Cycle: Recent Trends, Questions, and Potential Solutions. *Science* **320**, 889–892 (2008).
28. Steffen, W. *et al.* Sustainability. Planetary boundaries: guiding human development on a changing planet. *Science* **347**, 1259855 (2015).
29. Tilman, D. *et al.* Forecasting Agriculturally Driven Global Environmental Change. *Science* **292**, 281–284 (2001).
30. Silvertown, J. *et al.* The Park Grass Experiment 1856–2006: its contribution to ecology. *J. Ecol.* **94**, 801–814 (2006).
31. Fornara, D. A. & Tilman, D. Soil carbon sequestration in prairie grasslands increased by chronic nitrogen addition. *Ecology* **93**, 2030–2036 (2012).
32. Hamilton, S. K. Biogeochemical time lags may delay responses of streams to ecological restoration. *Freshw. Biol.* **57**, 43–57 (2012).
33. Lovett, G. M. *et al.* Nutrient retention during ecosystem succession: a revised conceptual model. *Front. Ecol. Environ.* **16**, 532–538 (2018).

34. Dodds, W. K. *et al.* Eutrophication of U.S. Freshwaters: Analysis of Potential Economic Damages. *Environ. Sci. Technol.* **43**, 12–19 (2009).
35. Keeler, B. L. *et al.* The social costs of nitrogen. *Sci. Adv.* **2**, e1600219 (2016).
36. Isbell, F. *et al.* Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proc. Natl. Acad. Sci.* **110**, 11911–11916 (2013).
37. Frey, S. D. *et al.* Chronic nitrogen additions suppress decomposition and sequester soil carbon in temperate forests. *Biogeochemistry* **121**, 305–316 (2014).
38. Smith, M. D. *et al.* Global environmental change and the nature of aboveground net primary productivity responses: insights from long-term experiments. *Oecologia* **177**, 935–947 (2015).
39. Gough, L. *et al.* Effects of long-term nutrient additions on Arctic tundra, stream, and lake ecosystems: beyond NPP. *Oecologia* **182**, 653–665 (2016).
40. Carson, C. M. & Zeglin, L. H. Long-term fire management history affects N-fertilization sensitivity, but not seasonality, of grassland soil microbial communities. *Soil Biol. Biochem.* **121**, 231–239 (2018).
41. Peterson, B. J. *et al.* Biological Responses of a Tundra River to Fertilization. *Ecology* **74**, 653–672 (1993).
42. Suding, K. N. *et al.* Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proc. Natl. Acad. Sci.* **102**, 4387–4392 (2005).
43. Farrer, E. C. *et al.* Indirect effects of global change accumulate to alter plant diversity but not ecosystem function in alpine tundra. *J. Ecol.* **103**, 351–360 (2015).
44. La Pierre, K. J. & Smith, M. D. Functional trait expression of grassland species shift with short- and long-term nutrient additions. *Plant Ecol.* **216**, 307–318 (2015).
45. Koerner, S. E. *et al.* Nutrient additions cause divergence of tallgrass prairie plant communities resulting in loss of ecosystem stability. *J. Ecol.* **104**, 1478–1487 (2016).
46. Bowman, W. D. *et al.* Limited ecosystem recovery from simulated chronic nitrogen deposition. *Ecol. Appl. Publ. Ecol. Soc. Am.* **28**, 1762–1772 (2018).
47. Rastetter, E. B., Ågren, G. I. & Shaver, G. R. Responses of N-Limited Ecosystems to Increased Co₂: A Balanced-Nutrition, Coupled-Element-Cycles Model. *Ecol. Appl.* **7**, 444–460 (1997).
48. Mack, M. C., Schuur, E. A. G., Bret-Harte, M. S., Shaver, G. R. & Chapin, F. S. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* **431**, 440–443 (2004).
49. Deegan, L. A. *et al.* Coastal eutrophication as a driver of salt marsh loss. *Nature* **490**, 388–392 (2012).

50. Likens, G. E., Driscoll, C. T. & Buso, D. C. Long-Term Effects of Acid Rain: Response and Recovery of a Forest Ecosystem. *Science* **272**, 244–246 (1996).
51. Carpenter, S. R., Booth, E. G. & Kucharik, C. J. Extreme precipitation and phosphorus loads from two agricultural watersheds. *Limnol. Oceanogr.* **63**, 1221–1233 (2018).
52. Rivera-Monroy, V. H. *et al.* The Life of P: A Biogeochemical and Sociopolitical Challenge in the Everglades. in *The Coastal Everglades: The Dynamics of Social-Ecological Transformation in the South Florida Landscape* (Oxford University Press, 2019).
53. Trexler, J. C., Gaiser, E. E., Kominoski, J. & Sanchez, J. L. The Role of Periphyton Mats in Consumer Community Structure and Function in Calcareous Wetlands: Lessons from the Everglades. in *Microbiology of the Everglades Ecosystem* 155–179 (CRC Press, 2015).
54. Hogle, S. L. *et al.* Pervasive iron limitation at subsurface chlorophyll maxima of the California Current. *Proc. Natl. Acad. Sci.* **115**, 13300–13305 (2018).
55. Walsh, J. R., Carpenter, S. R. & Zanden, M. J. V. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. *Proc. Natl. Acad. Sci.* **113**, 4081–4085 (2016).
56. Walsh, J. R., Lathrop, R. C. & Zanden, M. J. V. Invasive invertebrate predator, *Bythotrephes longimanus*, reverses trophic cascade in a north-temperate lake. *Limnol. Oceanogr.* **62**, 2498–2509 (2017).
57. Isbell, F., Tilman, D., Polasky, S., Binder, S. & Hawthorne, P. Low biodiversity state persists two decades after cessation of nutrient enrichment. *Ecol. Lett.* **16**, 454–460 (2013).
58. Johnson, D. S., Fleeger, J. W. & Deegan, L. A. Large-scale manipulations reveal that top-down and bottom-up controls interact to alter habitat utilization by saltmarsh fauna. *Mar. Ecol. Prog. Ser.* **377**, 33–41 (2009).
59. Fourqurean, J. W. *et al.* Seagrass ecosystems as a globally significant carbon stock. *Nat. Geosci.* **5**, 505–509 (2012).
60. Rovai, A. S. *et al.* Global controls on carbon storage in mangrove soils. *Nat. Clim. Change* **8**, 534–538 (2018).
61. Saha, A. K. *et al.* Sea level rise and South Florida coastal forests. *Clim. Change* **107**, 81–108 (2011).
62. Wilson, B. J. *et al.* Phosphorus alleviation of salinity stress: effects of saltwater intrusion on an Everglades freshwater peat marsh. *Ecology* **100**, e02672 (2019).
63. Castañeda-Moya, E. *et al.* Patterns of Root Dynamics in Mangrove Forests Along Environmental Gradients in the Florida Coastal Everglades, USA. *Ecosystems* **14**, 1178–1195 (2011).
64. Danielson, T. M. *et al.* Assessment of Everglades mangrove forest resilience: Implications for above-ground net primary productivity and carbon dynamics. *For. Ecol. Manag.* **404**, 115–125 (2017).

65. Breithaupt, J. L., Smoak, J. M., Sanders, C. J. & Troxler, T. G. Spatial Variability of Organic Carbon, CaCO₃ and Nutrient Burial Rates Spanning a Mangrove Productivity Gradient in the Coastal Everglades. *Ecosystems* **22**, 844–858 (2019).
66. Charles, S. P. *et al.* Experimental Saltwater Intrusion Drives Rapid Soil Elevation and Carbon Loss in Freshwater and Brackish Everglades Marshes. *Estuaries Coasts* (2019). doi:10.1007/s12237-019-00620-3
67. Clausing, R. J. & Fong, P. Environmental variability drives rapid and dramatic changes in nutrient limitation of tropical macroalgae with different ecological strategies. *Coral Reefs* **35**, 669–680 (2016).
68. Reich, P. B., Hobbie, S. E. & Lee, T. D. Plant growth enhancement by elevated CO₂ eliminated by joint water and nitrogen limitation. *Nat. Geosci.* **7**, 920–924 (2014).
69. Fay, P. A. *et al.* Grassland productivity limited by multiple nutrients. *Nat. Plants* **1**, 1–5 (2015).
70. Harpole, W. S. *et al.* Addition of multiple limiting resources reduces grassland diversity. *Nature* **537**, 93–96 (2016).
71. Borer, E. T., Grace, J. B., Harpole, W. S., MacDougall, A. S. & Seabloom, E. W. A decade of insights into grassland ecosystem responses to global environmental change. *Nat. Ecol. Evol.* **1**, 1–7 (2017).
72. La Pierre, K. J. L., Joern, A. & Smith, M. D. Invertebrate, not small vertebrate, herbivory interacts with nutrient availability to impact tallgrass prairie community composition and forb biomass. *Oikos* **124**, 842–850 (2015).
73. Lind, E. M. *et al.* Increased grassland arthropod production with mammalian herbivory and eutrophication: a test of mediation pathways. *Ecology* **98**, 3022–3033 (2017).
74. Elser, J. J. *et al.* Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* **10**, 1135–1142 (2007).
75. Gruner, D. S. *et al.* A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecol. Lett.* **11**, 740–755 (2008).
76. Harmon, M. E. *et al.* Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. *Glob. Change Biol.* **15**, 1320–1338 (2009).
77. Seabloom, E. W. *et al.* Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. *Nat. Commun.* **6**, 1–8 (2015).
78. Crowther, T. W. *et al.* Sensitivity of global soil carbon stocks to combined nutrient enrichment. *Ecol. Lett.* **22**, 936–945 (2019).
79. Bettez, N. D. *et al.* Climate Variation Overwhelms Efforts to Reduce Nitrogen Delivery to Coastal Waters. *Ecosystems* **18**, 1319–1331 (2015).

80. Gaiser, E. E. *et al.* Cascading ecological effects of low-level phosphorus enrichment in the Florida everglades. *J. Environ. Qual.* **34**, 717–723 (2005).
81. Shcherbak, I., Millar, N. & Robertson, G. P. Global metaanalysis of the nonlinear response of soil nitrous oxide (N₂O) emissions to fertilizer nitrogen. *Proc. Natl. Acad. Sci.* **111**, 9199–9204 (2014).
82. Luo, Y. *et al.* Progressive Nitrogen Limitation of Ecosystem Responses to Rising Atmospheric Carbon Dioxide. *BioScience* **54**, 731–739 (2004).
83. Connell, J. H. Effects of Competition, Predation by *Thais lapillus*, and Other Factors on Natural Populations of the Barnacle *Balanus balanoides*. *Ecol. Monogr.* **31**, 61–104 (1961).
84. Paine, R. T. Food Web Complexity and Species Diversity. *Am. Nat.* **100**, 65–75 (1966).
85. Estes, J. A. & Palmisano, J. F. Sea Otters: Their Role in Structuring Nearshore Communities. *Science* **185**, 1058–1060 (1974).
86. Collins, S. L., Knapp, A. K., Briggs, J. M., Blair, J. M. & Steinauer, E. M. Modulation of Diversity by Grazing and Mowing in Native Tallgrass Prairie. *Science* **280**, 745–747 (1998).
87. Carpenter, S. R. *et al.* Regulation of Lake Primary Productivity by Food Web Structure. *Ecology* **68**, 1863–1876 (1987).
88. Adam, T. C. *et al.* Herbivory, Connectivity, and Ecosystem Resilience: Response of a Coral Reef to a Large-Scale Perturbation. *PLOS ONE* **6**, e23717 (2011).
89. Raynor, E. J., Joern, A. & Briggs, J. M. Bison foraging responds to fire frequency in nutritionally heterogeneous grassland. *Ecology* **96**, 1586–1597 (2015).
90. Ling, B., Raynor, E. J., Goodin, D. G. & Joern, A. Effects of Fire and Large Herbivores on Canopy Nitrogen in a Tallgrass Prairie. *Remote Sens.* **11**, 1364 (2019).
91. O’Keefe, K. & Nippert, J. B. Grazing by bison is a stronger driver of plant ecohydrology in tallgrass prairie than fire history. *Plant Soil* **411**, 423–436 (2017).
92. Ratajczak, Z., Nippert, J. B., Briggs, J. M. & Blair, J. M. Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the Central Great Plains of North America. *J. Ecol.* **102**, 1374–1385 (2014).
93. Welti, E. A. R. *et al.* Fire, grazing and climate shape plant–grasshopper interactions in a tallgrass prairie. *Funct. Ecol.* **33**, 735–745 (2019).
94. Koerner, S. E. *et al.* Plant community response to loss of large herbivores differs between North American and South African savanna grasslands. *Ecology* **95**, 808–816 (2014).
95. Olnes, J. & Kielland, K. Stage-dependent effects of browsing by snowshoe hares on successional dynamics in a boreal forest ecosystem. *Ecosphere* **7**, e01475 (2016).

96. Olnes, J. & Kielland, K. Asynchronous recruitment dynamics of snowshoe hares and white spruce in a boreal forest. *For. Ecol. Manag.* **384**, 83–91 (2017).
97. Olnes, J. *et al.* Can snowshoe hares control treeline expansions? *Ecology* **98**, 2506–2512 (2017).
98. Krebs, C. J. *et al.* Synchrony in the snowshoe hare (*Lepus americanus*) cycle in northwestern North America, 1970–2012. *Can. J. Zool.* **91**, 562–572 (2013).
99. Krebs, C. J. *et al.* What factors determine cyclic amplitude in the snowshoe hare (*Lepus americanus*) cycle? *Can. J. Zool.* **92**, 1039–1048 (2014).
100. Kielland, K., Olson, K. & Euskirchen, E. Demography of snowshoe hares in relation to regional climate variability during a 10-year population cycle in interior Alaska. *Can. J. For. Res.* **40**, 1265–1272 (2009).
101. Feierabend, D. & Kielland, K. Seasonal Effects of Habitat on Sources and Rates of Snowshoe Hare Predation in Alaskan Boreal Forests. *PLOS ONE* **10**, e0143543 (2015).
102. Matich, P. *et al.* Ecological niche partitioning within a large predator guild in a nutrient-limited estuary. *Limnol. Oceanogr.* **62**, 934–953 (2017).
103. Boucek, R. E. & Rehage, J. S. No free lunch: displaced marsh consumers regulate a prey subsidy to an estuarine consumer. *Oikos* **122**, 1453–1464 (2013).
104. Matich, P. & Heithaus, M. R. Multi-tissue stable isotope analysis and acoustic telemetry reveal seasonal variability in the trophic interactions of juvenile bull sharks in a coastal estuary. *J. Anim. Ecol.* **83**, 199–213 (2014).
105. Nifong, J. C. & Silliman, B. Abiotic factors influence the dynamics of marine habitat use by a highly mobile “freshwater” top predator. *Hydrobiologia* **802**, 155–174 (2017).
106. Rosenblatt, A. *et al.* The Roles of Large Top Predators in Coastal Ecosystems: New Insights from Long Term Ecological Research. *Oceanography* **26**, 156–167 (2013).
107. Mather, M. E., Finn, J. T., Kennedy, C. G., Deegan, L. A. & Smith, J. M. What happens in an estuary doesn’t stay there: patterns of biotic connectivity resulting from long term ecological research. *Oceanography* **26**, 12 (2013).
108. Dirzo, R. *et al.* Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
109. McCauley, D. J. *et al.* Marine defaunation: Animal loss in the global ocean. *Science* **347**, 1255641 (2015).
110. Rassweiler, A. *et al.* Perceptions and responses of Pacific Island fishers to changing coral reefs. *Ambio* (2019). doi:10.1007/s13280-019-01154-5
111. Bernes, C. *et al.* What is the influence of a reduction of planktivorous and benthivorous fish on water quality in temperate eutrophic lakes? A systematic review. *Environ. Evid.* **4**, 7 (2015).

112. Atwood, T. B. *et al.* Predators help protect carbon stocks in blue carbon ecosystems. *Nat. Clim. Change* **5**, 1038–1045 (2015).
113. Foster, D. *et al.* The Importance of Land-Use Legacies to Ecology and Conservation. *BioScience* **53**, 77–88 (2003).
114. Havstad, K. & Schlesinger, W. Reflections on a century of rangeland research in the Jornada Basin of New Mexico. in *Shrubland Ecosystem Dynamics in a changing environment* (eds. Barrow, J. R., McArthur, D. E., Sosebee, R. & Tausch, R. J.) 10–15 (USDA Forest Service, Intermountain Research Station, Gen. Tech. Rep. INT-GTR-338, 1995).
115. Foster, D. R., Fluet, M. & Boose, E. Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. *Ecol. Appl.* **9**, 555–572 (1999).
116. Thompson, J. *et al.* Land use history, environment, and tree composition in a tropical forest. *Ecol. Appl.* **12**, 1344–1363 (2002).
117. Johnstone, J. F. *et al.* Changing disturbance regimes, ecological memory, and forest resilience. *Front. Ecol. Environ.* **14**, 369–378 (2016).
118. Ratajczak, Z. *et al.* Abrupt Change in Ecological Systems: Inference and Diagnosis. *Trends Ecol. Evol.* **33**, 513–526 (2018).
119. Driscoll, C. T. *et al.* Acidic Deposition in the Northeastern United States: Sources and Inputs, Ecosystem Effects, and Management Strategies The effects of acidic deposition in the northeastern United States include the acidification of soil and water, which stresses terrestrial and aquatic biota. *BioScience* **51**, 180–198 (2001).
120. Battles, J. J., Fahey, T. J., Driscoll, C. T., Blum, J. D. & Johnson, C. E. Restoring Soil Calcium Reverses Forest Decline. *Environ. Sci. Technol. Lett.* **1**, 15–19 (2014).
121. Rosi-Marshall, E. J., Bernhardt, E. S., Buso, D. C., Driscoll, C. T. & Likens, G. E. Acid rain mitigation experiment shifts a forested watershed from a net sink to a net source of nitrogen. *Proc. Natl. Acad. Sci.* **113**, 7580–7583 (2016).
122. Lajtha, K. & Jones, J. Forest harvest legacies control dissolved organic carbon export in small watersheds, western Oregon. *Biogeochemistry* **140**, 299–315 (2018).
123. Walker, X. J. *et al.* Increasing wildfires threaten historic carbon sink of boreal forest soils. *Nature* **572**, 520–523 (2019).
124. Johnstone, J. F., Hollingsworth, T. N., Chapin, F. S. & Mack, M. C. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Glob. Change Biol.* **164** 1281–1295 (2009). doi:10.1111/j.1365-2486.2009.02051.x
125. Alexander, H. D. & Mack, M. C. A Canopy Shift in Interior Alaskan Boreal Forests: Consequences for Above- and Belowground Carbon and Nitrogen Pools during Post-fire Succession. *Ecosystems* **19**, 98–114 (2016).

126. Biggs, R., Carpenter, S., Brock, W. & Brock, W. Turning back from the brink: detecting an impending regime shift in time to avert it. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 826–831 (2008).
127. Hansen, G. J. A., Ives, A. R., Vander Zanden, M. J. & Carpenter, S. R. Are rapid transitions between invasive and native species caused by alternative stable states, and does it matter? *Ecology* **94**, 2207–2219 (2013).
128. Lathrop, R. C. & Carpenter, S. R. Water quality implications from three decades of phosphorus loads and trophic dynamics in the Yahara chain of lakes. *Inland Waters* **4**, 1–14 (2014).
129. Foster, D. R., Aber, J. D., Melillo, J. M., Bowden, R. D. & Bazzaz, F. A. Forest Response to Disturbance and Anthropogenic Stress. *BioScience* **47**, 437–445 (1997).
130. Castañeda-Moya, E. *et al.* Sediment and Nutrient Deposition Associated with Hurricane Wilma in Mangroves of the Florida Coastal Everglades. *Estuaries Coasts* **33**, 45–58 (2010).
131. Hogan, J. A., Zimmerman, J. K., Thompson, J., Nytech, C. J. & Uriarte, M. The interaction of land-use legacies and hurricane disturbance in subtropical wet forest: twenty-one years of change. *Ecosphere* **7**, e01405 (2016).
132. Peters, D. P. C. *et al.* Cross-system comparisons elucidate disturbance complexities and generalities. *Ecosphere* **2**, art81 (2011).
133. Likens, G. E. The role of science in decision making: does evidence-based science drive environmental policy? *Front. Ecol. Environ.* **8**, e1–e9 (2010).
134. Schmalensee, R. & Stavins, R. N. Lessons Learned from Three Decades of Experience with Cap and Trade. *Rev. Environ. Econ. Policy* **11**, 59–79 (2017).
135. Baron, J. S., Driscoll, C. T., Stoddard, J. L. & Richer, E. E. Empirical Critical Loads of Atmospheric Nitrogen Deposition for Nutrient Enrichment and Acidification of Sensitive US Lakes. *BioScience* **61**, 602–613 (2011).
136. Lindenmayer, D. B. *et al.* Salvage Harvesting Policies After Natural Disturbance. *Science* **303**, 1303–1303 (2004).
137. Foster, D. *et al.* *Wildlands and Woodlands: A Vision for the New England Landscape*. (Harvard Forest; Harvard University Press, 2010).
138. Thomas, J. W., Franklin, J. E., Gordon, J. & Johnson, K. N. The Northwest Forest Plan: origins, components, implementation experience, and suggestions for change. *Conserv. Biol. J. Soc. Conserv. Biol.* **20**, 277–287 (2006).
139. Phalan, B. T. *et al.* Impacts of the Northwest Forest Plan on forest composition and bird populations. *Proc. Natl. Acad. Sci.* **116**, 3322–3327 (2019).
140. Elton, C. *The Ecology of Invasions by Animals and Plants*. (University of Chicago Press; New edition edition (June 15, 2000), 1958).

141. May, R. *Stability and Complexity in Model Ecosystems*. (Princeton University Press, 1973).
142. McNaughton, S. J. Diversity and Stability of Ecological Communities: A Comment on the Role of Empiricism in Ecology. *Am. Nat.* **111**, 515–525 (1977).
143. Vandermeer, J., Lawrence, D., Symstad, A., Hobbie, H. & Inchausti, P. Effect of biodiversity on ecosystem functioning in managed ecosystems. in *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives* (eds. Loreau, M. & Naeem, S.) 221–236 (Oxford University Press, 2002).
144. *Biodiversity and Ecosystem Function*. (Springer-Verlag, 1994).
145. Tilman, D., Isbell, F. & Cowles, J. M. Biodiversity and Ecosystem Functioning. *Annu. Rev. Ecol. Evol. Syst.* **45**, 471–493 (2014).
146. Tilman, D. *et al.* Diversity and Productivity in a Long-Term Grassland Experiment. *Science* **294**, 843–845 (2001).
147. Tilman, D., Reich, P. B. & Knops, J. M. H. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**, 629–632 (2006).
148. Kennedy, T. A. *et al.* Biodiversity as a barrier to ecological invasion. *Nature* **417**, 636–638 (2002).
149. Tilman, D., Lehman, C. L. & Bristow, C. E. Diversity-stability relationships: statistical inevitability or ecological consequence? *Am. Nat.* **151**, 277–282 (1998).
150. Lehman, C. L. & Tilman, D. Biodiversity, Stability, and Productivity in Competitive Communities. *Am. Nat.* **156**, 534–552 (2000).
151. Fargione, J. *et al.* From selection to complementarity: shifts in the causes of biodiversity–productivity relationships in a long-term biodiversity experiment. *Proc. R. Soc. B Biol. Sci.* **274**, 871–876 (2007).
152. O’Connor, M. I. *et al.* A general biodiversity–function relationship is mediated by trophic level. *Oikos* **126**, 18–31 (2017).
153. Reich, P. B. *et al.* Impacts of Biodiversity Loss Escalate Through Time as Redundancy Fades. *Science* **336**, 589–592 (2012).
154. Smith, R. G., Gross, K. L. & Robertson, G. P. Effects of Crop Diversity on Agroecosystem Function: Crop Yield Response. *Ecosystems* **11**, 355–366 (2008).
155. Yang, Y., Tilman, D., Furey, G. & Lehman, C. Soil carbon sequestration accelerated by restoration of grassland biodiversity. *Nat. Commun.* **10**, 1–7 (2019).
156. Cline, L. C. *et al.* Resource availability underlies the plant-fungal diversity relationship in a grassland ecosystem. *Ecology* **99**, 204–216 (2018).

157. Tiemann, L. K., Grandy, A. S., Atkinson, E. E., Marin-Spiotta, E. & McDaniel, M. D. Crop rotational diversity enhances belowground communities and functions in an agroecosystem. *Ecol. Lett.* **18**, 761–771 (2015).
158. Tilman, D., Reich, P. B. & Isbell, F. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proc. Natl. Acad. Sci.* **109**, 10394–10397 (2012).
159. Zavaleta, E. S., Pasari, J. R., Hulvey, K. B. & Tilman, G. D. Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proc. Natl. Acad. Sci.* **107**, 1443–1446 (2010).
160. Isbell, F. *et al.* High plant diversity is needed to maintain ecosystem services. *Nature* **477**, 199–202 (2011).
161. Loreau, M. & Hector, A. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**, 72–76 (2001).
162. Hector, A. *et al.* Plant Diversity and Productivity Experiments in European Grasslands. *Science* **286**, 1123–1127 (1999).
163. Kirwan, L. *et al.* Evenness drives consistent diversity effects in intensive grassland systems across 28 European sites. *J. Ecol.* **95**, 530–539 (2007).
164. Verheyen, K. *et al.* Contributions of a global network of tree diversity experiments to sustainable forest plantations. *Ambio* **45**, 29–41 (2016).
165. Grossman, J. J. *et al.* Synthesis and future research directions linking tree diversity to growth, survival, and damage in a global network of tree diversity experiments. *Environ. Exp. Bot.* **152**, 68–89 (2018).
166. Stachowicz, J. J. & Byrnes, J. E. Species diversity, invasion success, and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors. *Mar. Ecol. Prog. Ser.* **311**, 251–262 (2006).
167. Cardinale, B. J. *et al.* Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. *Ecology* **94**, 1697–1707 (2013).
168. Cadotte, M. W., Cavender-Bares, J., Tilman, D. & Oakley, T. H. Using Phylogenetic, Functional and Trait Diversity to Understand Patterns of Plant Community Productivity. *PLOS ONE* **4**, e5695 (2009).
169. Grossman, J. J., Cavender-Bares, J., Hobbie, S. E., Reich, P. B. & Montgomery, R. A. Species richness and traits predict overyielding in stem growth in an early-successional tree diversity experiment. *Ecology* **98**, 2601–2614 (2017).
170. Schweiger, A. K. *et al.* Plant spectral diversity integrates functional and phylogenetic components of biodiversity and predicts ecosystem function. *Nat. Ecol. Evol.* **2**, 976–982 (2018).

171. Steltzer, H. & Bowman, W. D. Original Articles: Differential Influence of Plant Species on Soil Nitrogen Transformations Within Moist Meadow Alpine Tundra. *Ecosystems* **1**, 464–474 (1998).
172. Meier, C. L. & Bowman, W. D. Links between plant litter chemistry, species diversity, and below-ground ecosystem function. *Proc. Natl. Acad. Sci.* **105**, 19780–19785 (2008).
173. Smith, M. D. & Knapp, A. K. Dominant species maintain ecosystem function with non-random species loss. *Ecol. Lett.* **6**, 509–517 (2003).
174. Jackson, C. R. *et al.* Unexpected ecological advances made possible by long-term data: A Coweeta example. *Wiley Interdiscip. Rev. Water* **5**, e1273 (2018).
175. Peters, J. R., Reed, D. C. & Burkepille, D. E. Climate and fishing drive regime shifts in consumer-mediated nutrient cycling in kelp forests. *Glob. Change Biol.* **25**, 3179–3192 (2019).
176. Miller, R. J. *et al.* Giant kelp, *Macrocystis pyrifera*, increases faunal diversity through physical engineering. *Proc. Biol. Sci.* **285**, (2018).
177. Crotty, S. M. *et al.* Foundation species patch configuration mediates salt marsh biodiversity, stability and multifunctionality. *Ecol. Lett.* **21**, 1681–1692 (2018).
178. Orwig, D. A. *et al.* Foundation species loss affects vegetation structure more than ecosystem function in a northeastern USA forest. *PeerJ* **1**, e41 (2013).
179. Ellison, A. M., Barker-Plotkin, A. A., Foster, D. R. & Orwig, D. A. Experimentally testing the role of foundation species in forests: the Harvard Forest Hemlock Removal Experiment. *Methods Ecol. Evol.* **1**, 168–179 (2010).
180. Carr, J. A., D’Odorico, P., McGlathery, K. J. & Wiberg, P. L. Stability and resilience of seagrass meadows to seasonal and interannual dynamics and environmental stress. *J. Geophys. Res. Biogeosciences* **117**, (2012).
181. Oreska, M. P. J., McGlathery, K. J. & Porter, J. H. Seagrass blue carbon spatial patterns at the meadow-scale. *PLOS ONE* **12**, e0176630 (2017).
182. Isbell, F. *et al.* Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* **526**, 574–577 (2015).
183. Hautier, Y. *et al.* Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science* **348**, 336–340 (2015).
184. Grace, J. B. *et al.* Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature* **529**, 390–393 (2016).
185. Liang, J. *et al.* Positive biodiversity-productivity relationship predominant in global forests. *Science* **354**, aaf8957 (2016).
186. Cavender-Bares, J. *et al.* Harnessing plant spectra to integrate the biodiversity sciences across biological and spatial scales. *Am. J. Bot.* **104**, 966–969 (2017).

187. Isbell, F. *et al.* Linking the influence and dependence of people on biodiversity across scales. *Nature* **546**, 65–72 (2017).
188. Isbell, F. *et al.* Benefits of increasing plant diversity in sustainable agroecosystems. *J. Ecol.* **105**, 871–879 (2017).
189. Binder, S., Isbell, F., Polasky, S., Catford, J. A. & Tilman, D. Grassland biodiversity can pay. *Proc. Natl. Acad. Sci.* **115**, 3876–3881 (2018).
190. Werling, B. P. *et al.* Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. *Proc. Natl. Acad. Sci.* **111**, 1652–1657 (2014).
191. Burgess, M. G. Consequences of fleet diversification in managed and unmanaged fisheries. *Can. J. Fish. Aquat. Sci.* **72**, 54–70 (2014).
192. Renard, D. & Tilman, D. National food production stabilized by crop diversity. *Nature* **571**, 257–260 (2019).
193. Leis, J. M. Are Larvae of Demersal Fishes Plankton or Nekton? in *Advances in Marine Biology* **51**, 57–141 (Academic Press, 2006).
194. Taylor, P. D., Fahrig, L., Henein, K. & Merriam, G. Connectivity Is a Vital Element of Landscape Structure. *Oikos* **68**, 571–573 (1993).
195. Pringle, C. M. Hydrologic Connectivity and the Management of Biological Reserves: A Global Perspective. *Ecol. Appl.* **11**, 981–998 (2001).
196. Aguilera, R. & Melack, J. M. Relationships Among Nutrient and Sediment Fluxes, Hydrological Variability, Fire, and Land Cover in Coastal California Catchments. *J. Geophys. Res. Biogeosciences* **123**, 2568–2589 (2018).
197. Morrow, R. M. *et al.* CCE V: Primary production, mesozooplankton grazing, and the biological pump in the California Current Ecosystem: Variability and response to El Niño. *Deep Sea Res. Part Oceanogr. Res. Pap.* **140**, 52–62 (2018).
198. Kendrick, M. R. *et al.* Linking permafrost thaw to shifting biogeochemistry and food web resources in an arctic river. *Glob. Change Biol.* **24**, 5738–5750 (2018).
199. O'Donnell, J. P. R. & Schalles, J. F. Examination of Abiotic Drivers and Their Influence on *Spartina alterniflora* Biomass over a Twenty-Eight Year Period Using Landsat 5 TM Satellite Imagery of the Central Georgia Coast. *Remote Sens.* **8**, 477 (2016).
200. Castorani, M. C. N. *et al.* Connectivity structures local population dynamics: a long-term empirical test in a large metapopulation system. *Ecology* **96**, 3141–3152 (2015).
201. Castorani, M. C. N. *et al.* Fluctuations in population fecundity drive variation in demographic connectivity and metapopulation dynamics. *Proc. Biol. Sci.* **284**, (2017).

202. Garcia-Moya, E. & McKell, C. M. Contribution of Shrubs to the Nitrogen Economy of a Desert-Wash Plant Community. *Ecology* **51**, 81–88 (1970).
203. Schlesinger, W. H. *et al.* Biological Feedbacks in Global Desertification. *Science* **247**, 1043–1048 (1990).
204. Okin, G. S. *et al.* Connectivity in dryland landscapes: shifting concepts of spatial interactions. *Front. Ecol. Environ.* **13**, 20–27 (2015).
205. Bracken, L. J. *et al.* Concepts of hydrological connectivity: Research approaches, pathways and future agendas. *Earth-Sci. Rev.* **119**, 17–34 (2013).
206. Crump, B. C., Amaral-Zettler, L. A. & Kling, G. W. Microbial diversity in arctic freshwaters is structured by inoculation of microbes from soils. *ISME J.* **6**, 1629–1639 (2012).
207. Cloern, J. E. Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.* **210**, 223–253 (2001).
208. Więski, K. & Pennings, S. C. Climate Drivers of *Spartina alterniflora* Saltmarsh Production in Georgia, USA. *Ecosystems* **17**, 473–484 (2014).
209. Morris, J. T., Kjerfve, B. & Dean, J. M. Dependence of estuarine productivity on anomalies in mean sea level. *Limnol. Oceanogr.* **35**, 926–930 (1990).
210. Kirwan, M. L., Christian, R. R., Blum, L. K. & Brinson, M. M. On the Relationship Between Sea Level and *Spartina alterniflora* Production. *Ecosystems* **15**, 140–147 (2012).
211. Collins, S. L. *et al.* An integrated conceptual framework for long-term social–ecological research. *Front. Ecol. Environ.* **9**, 351–357 (2011).
212. Clark, W. C. Sustainability Science: A room of its own. *Proc. Natl. Acad. Sci.* **104**, 1737–1738 (2007).
213. Liu, J. *et al.* Complexity of Coupled Human and Natural Systems. *Science* **317**, 1513–1516 (2007).
214. Ostrom, E. A General Framework for Analyzing Sustainability of Social-Ecological Systems. *Science* **325**, 419–422 (2009).
215. Groffman, P. M. *et al.* Moving Towards a New Urban Systems Science. *Ecosystems* **20**, 38–43 (2017).
216. Robertson, G. P. *et al.* Long-Term Ecological Research in a Human-Dominated World. *BioScience* **62**, 342–353 (2012).
217. Robertson, P. G. *et al.* Farming for Ecosystem Services: An Ecological Approach to Production Agriculture. *BioScience* **64**, 404–415 (2014).

218. Childers, D. L., Gaiser, E. & Ogden, L. A. *The Coastal Everglades: The Dynamics of Social-Ecological Transformation in the South Florida Landscape*. (Oxford University Press, 2019).
219. Thompson, J. R. *et al.* Scenario Studies as a Synthetic and Integrative Research Activity for Long-Term Ecological Research. *BioScience* **62**, 367–376 (2012).
220. Groffman, P. M. *et al.* Ecological homogenization of residential macrosystems. *Nat. Ecol. Evol.* **1**, 0191 (2017).
221. Cook, E. M., Hall, S. J. & Larson, K. L. Residential landscapes as social-ecological systems: a synthesis of multi-scalar interactions between people and their home environment. *Urban Ecosyst.* **15**, 19–52 (2012).
222. Childers, D. L., Pickett, S. T. A., Grove, J. M., Ogden, L. & Whitmer, A. Advancing urban sustainability theory and action: Challenges and opportunities. *Landsc. Urban Plan.* **125**, 320–328 (2014).
223. Childers, D. L. *et al.* An ecology for cities: A transformational nexus of design and ecology to advance climate change resilience and urban sustainability. *Sustain. Spec. Issue Sustain. Urban Dev.* **7** 3774-3791 **7**, 3774–3791 (2015).
224. Hamilton, S. K. & Robertson, G. P. *The Ecology of Agricultural Landscapes: Long-term Research on the Path to Sustainability*. (Oxford University Press, 2015).
225. McPhearson, T. *et al.* Advancing Urban Ecology toward a Science of Cities. *BioScience* **66**, 198–212 (2016).
226. Pickett, S. T. A., Cadenasso, M. L., Childers, D. L., McDonnell, M. J. & Zhou, W. Evolution and future of urban ecological science: ecology in, of, and for the city. *Ecosyst. Health Sustain.* **2**, e01229 (2016).
227. Grimm, N. B., Pickett, S. T. A., Hale, R. L. & Cadenasso, M. L. Does the ecological concept of disturbance have utility in urban social–ecological–technological systems? *Ecosyst. Health Sustain.* **3**, e01255 (2017).
228. Hager, G. W. *et al.* Socioecological revitalization of an urban watershed. *Front. Ecol. Environ.* **11**, 28–36 (2013).
229. Ripplinger, J., Franklin, J. & Collins, S. L. When the economic engine stalls – A multi-scale comparison of vegetation dynamics in pre- and post-recession Phoenix, Arizona, USA. *Landsc. Urban Plan.* **153**, 140–148 (2016).
230. Ripplinger, J., Collins, S. L., York, A. M. & Franklin, J. Boom–bust economics and vegetation dynamics in a desert city: How strong is the link? *Ecosphere* **8**, e01826 (2017).
231. Bang, C., Faeth, S. H. & Sabo, J. L. Control of arthropod abundance, richness, and composition in a heterogeneous desert city. *Ecol. Monogr.* **82**, 85–100 (2012).
232. Banville, M. J., Bateman, H. L., Earl, S. R. & Warren, P. S. Decadal declines in bird abundance and diversity in urban riparian zones. *Landsc. Urban Plan.* **159**, 48–61 (2017).

233. Palta, M., du Bray, M. V., Stotts, R., Wolf, A. & Wutich, A. Ecosystem Services and Disservices for a Vulnerable Population: Findings from Urban Waterways and Wetlands in an American Desert City. *Hum. Ecol.* **44**, 463–478 (2016).
234. Markowski-Lindsay, M. *et al.* Compounding the Disturbance: Family Forest Owner Reactions to Invasive Forest Insects. *Ecol. Econ.* **167**, 106461 (2020).
235. Ma, S., Swinton, S. M., Lupi, F. & Jolejole-Foreman, C. Farmers' Willingness to Participate in Payment-for-Environmental-Services Programmes. *J. Agric. Econ.* **63**, 604–626 (2012).
236. Enquist, C. A. *et al.* Foundations of translational ecology. *Front. Ecol. Environ.* **15**, 541–550 (2017).
237. Thompson, J. R. *et al.* Scenario Studies as a Synthetic and Integrative Research Activity for Long-Term Ecological Research. *BioScience* **62**, 367–376 (2012).
238. Bestelmeyer, B. T. *et al.* Analysis of abrupt transitions in ecological systems. *Ecosphere* **2**, art129 (2011).
239. Scheffer, M. *et al.* Anticipating Critical Transitions. *Science* **338**, 344–348 (2012).
240. Schmitt, R. J., Holbrook, S. J., Davis, S. L., Brooks, A. J. & Adam, T. C. Experimental support for alternative attractors on coral reefs. *Proc. Natl. Acad. Sci.* **116**, 4372–4381 (2019).
241. Bestelmeyer, B. T., Duniway, M. C., James, D. K., Burkett, L. M. & Havstad, K. M. A test of critical thresholds and their indicators in a desertification-prone ecosystem: more resilience than we thought. *Ecol. Lett.* **16**, 339–345 (2013).
242. McGlathery, K. *et al.* Recovery trajectories during state change from bare sediment to eelgrass dominance. *Mar. Ecol. Prog. Ser.* **448**, 209–221 (2012).
243. Orth, R. & McGlathery, K. Eelgrass recovery in the coastal bays of the Virginia Coast Reserve, USA. *Mar. Ecol. Prog. Ser.* **448**, 173–176 (2012).
244. Berg, P. *et al.* Non-invasive flux Measurements at the Benthic Interface: The Aquatic Eddy Covariance Technique. *Limnol. Oceanogr. E-Lect.* **7**, 1–50 (2017).
245. Berg, P. *et al.* Dynamics of benthic metabolism, O₂, and pCO₂ in a temperate seagrass meadow. *Limnol. Oceanogr.* **0**,
246. Aoki, L. R., McGlathery, K. J., Wiberg, P. L. & Al-Haj, A. Depth affects seagrass restoration success and resilience to marine heat wave disturbance. *Estuaries Coasts* **In Review**,
247. Edmunds, P. J. Implications of high rates of sexual recruitment in driving rapid reef recovery in Moorea, French Polynesia. *Sci. Rep.* **8**, 1–11 (2018).
248. Han, X., Adam, T. C., Schmitt, R. J., Brooks, A. J. & Holbrook, S. J. Response of herbivore functional groups to sequential perturbations in Moorea, French Polynesia. *Coral Reefs* **35**, 999–1009 (2016).

249. Everham, E. M. & Brokaw, N. V. L. Forest damage and recovery from catastrophic wind. *Bot. Rev.* **62**, 113–185 (1996).
250. Scatena, F. N. *et al.* Disturbance Regime. in *A Caribbean forest tapestry: the multidimensional nature of disturbance and response* (eds. Brokaw *et al.*) 164–200 (Oxford University Press, 2012).
251. Fraza, E. & Elsner, J. B. A spatial climatology of North Atlantic hurricane intensity change. *Int. J. Climatol.* **34**, 2918–2924 (2014).
252. Emanuel, K. Will Global Warming Make Hurricane Forecasting More Difficult? *Bull. Am. Meteorol. Soc.* **98**, 495–501 (2016).
253. Boose, E. R., Serrano, M. I. & Foster, D. R. LANDSCAPE AND REGIONAL IMPACTS OF HURRICANES IN PUERTO RICO. *Ecol. Monogr.* **74**, 335–352 (2004).
254. Foster, D. R. & Boose, E. R. Hurricane disturbance regimes in temperate and tropical forest ecosystems. in *Wind and Trees* (eds. Coutts, M. & Grace, J.) 305–339 (Cambridge University Press, 1995).
255. Zimmerman, J. K., Willig, M. R., Walker, L. R. & Silver, W. L. Introduction: Disturbance and Caribbean Ecosystems. *Biotropica* **28**, 414–423 (1996).
256. *A Caribbean Forest Tapestry: The Multidimensional Nature of Disturbance and Response.* (Oxford University Press, 2012).
257. McDowell, W. H. *et al.* Interactions between lithology and biology drive the long-term response of stream chemistry to major hurricanes in a tropical landscape. *Biogeochemistry* **116**, 175–186 (2013).
258. Scalley, T. H., Scatena, F. N., Lugo, A. E., Moya, S. & Ruiz, C. R. E. Changes in Structure, Composition, and Nutrients During 15 Yr of Hurricane-Induced Succession in a Subtropical Wet Forest in Puerto Rico. *Biotropica* **42**, 455–463 (2010).
259. Willig, M. R., Presley, S. J. & Bloch, C. P. Long-term dynamics of tropical walking sticks in response to multiple large-scale and intense disturbances. *Oecologia* **165**, 357–368 (2011).
260. Walker, L. R., Lodge, D. J., Brokaw, N. V. L. & Waide, R. B. An Introduction to Hurricanes in the Caribbean. *Biotropica* **23**, 313–316 (1991).
261. Walker, L. A., Silver, M. L., Willig, M. R. & Zimmerman, J. K. Special Issue: Long-term responses of Caribbean ecosystems to disturbance. *Biotropica* **28**,
262. Shiels, A. B. & Gonzalez, G. Understanding the key mechanisms of tropical forest responses to canopy loss and biomass deposition from experimental hurricane effects. *For. Ecol. Manag.* **332** 1–10 [Doi10.1016/j.foreco.2014.04.024](https://doi.org/10.1016/j.foreco.2014.04.024) **332**, 1–10 (2014).
263. Crowl, T. A. *et al.* When and where biota matter, linking disturbance regime, species characteristics, and dynamics of communities and ecosystems. in *A Caribbean forest tapestry: the multidimensional nature of disturbance and response* (eds. Lugo, A. E. *et al.*) (Oxford University Press, 2012).

264. Shiels, A. B., Gonzalez, G., Lodge, D. J., Willig, M. R. & Zimmerman, J. K. Cascading Effects of Canopy Opening and Debris Deposition from a Large-Scale Hurricane Experiment in a Tropical Rain Forest. (2015).
265. Wood, T., González, G., Silver, W., Reed, S. & Cavaleri, M. On the Shoulders of Giants: Continuing the Legacy of Large-Scale Ecosystem Manipulation Experiments in Puerto Rico. *Forests* **10**, 210 (2019).
266. Doran, P. T. *et al.* Antarctic climate cooling and terrestrial ecosystem response. *Nature* **415**, 517–520 (2002).
267. Gooseff, M. N. *et al.* Decadal ecosystem response to an anomalous melt season in a polar desert in Antarctica. *Nat. Ecol. Evol.* **1**, 1334–1338 (2017).
268. Kohler, T. J., Chatfield, E., Gooseff, M. N., Barrett, J. E. & McKnight, D. M. Recovery of Antarctic stream epilithon from simulated scouring events. *Antarct. Sci.* **27**, 341–354 (2015).
269. Wade, M. J. & Kalisz, S. THE CAUSES OF NATURAL SELECTION. *Evol. Int. J. Org. Evol.* **44**, 1947–1955 (1990).
270. MacColl, A. D. C. The ecological causes of evolution. *Trends Ecol. Evol.* **26**, 514–522 (2011).
271. Blount, Z. D., Borland, C. Z. & Lenski, R. E. Historical contingency and the evolution of a key innovation in an experimental population of *Escherichia coli*. *Proc. Natl. Acad. Sci.* **105**, 7899–7906 (2008).
272. Wisser, M. J., Ribeck, N. & Lenski, R. E. Long-Term Dynamics of Adaptation in Asexual Populations. *Science* **342**, 1364–1367 (2013).
273. Whitney, K. D. *et al.* Experimental drought reduces genetic diversity in the grassland foundation species *Bouteloua eriopoda*. *Oecologia* **189**, 1107–1120 (2019).
274. Shaw, E. C., Carpenter, R. C., Lantz, C. A. & Edmunds, P. J. Intraspecific variability in the response to ocean warming and acidification in the scleractinian coral *Acropora pulchra*. *Mar. Biol.* **163**, 210 (2016).
275. Weese, D. J., Heath, K. D., Dentinger, B. T. M. & Lau, J. A. Long-term nitrogen addition causes the evolution of less-cooperative mutualists. *Evolution* **69**, 631–642 (2015).
276. Klinger, C. R., Lau, J. A. & Heath, K. D. Ecological genomics of mutualism decline in nitrogen-fixing bacteria. *Proc. R. Soc. B Biol. Sci.* **283**, 20152563 (2016).
277. Lau, J. A. *et al.* Contemporary evolution influences soil nitrogen availability in experimental mesocosms. *Ecology* **In Review**,
278. Koskella, B. & Vos, M. Adaptation in Natural Microbial Populations. *Annu. Rev. Ecol. Evol. Syst.* **46**, 503–522 (2015).

279. de Mazancourt, C., Johnson, E. & Barraclough, T. G. Biodiversity inhibits species' evolutionary responses to changing environments. *Ecol. Lett.* **11**, 380–388 (2008).
280. Osmond, M. M., Otto, S. P. & Klausmeier, C. A. When Predators Help Prey Adapt and Persist in a Changing Environment. *Am. Nat.* **190**, 83–98 (2017).
281. Kleyhans, E. J., Otto, S. P., Reich, P. B. & Vellend, M. Adaptation to elevated CO₂ in different biodiversity contexts. *Nat. Commun.* **7**, 12358 (2016).
282. van Diepen, L. T. A., Frey, S. D., Landis, E. A., Morrison, E. W. & Pringle, A. Fungi exposed to chronic nitrogen enrichment are less able to decay leaf litter. *Ecology* **98**, 5–11 (2017).
283. Ellner, S. P., Geber, M. A. & Hairston, N. G. Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. *Ecol. Lett.* **14**, 603–614 (2011).
284. Hendry, A. P. A critique for eco-evolutionary dynamics. *Funct. Ecol.* **33**, 84–94 (2019).
285. Darwin, C. R. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.* (John Murray, 1859).
286. Hutchinson, G. E. *The ecological theater and the evolutionary play.* (Yale University Press, 1965).
287. Schluter, D., Clifford, E. A., Nemethy, M. & McKinnon, J. S. Parallel evolution and inheritance of quantitative traits. *Am. Nat.* **163**, 809–822 (2004).
288. Alberti, M. Eco-evolutionary dynamics in an urbanizing planet. *Trends Ecol. Evol.* **30**, 114–126 (2015).
289. Donihue, C. M. & Lambert, M. R. Adaptive evolution in urban ecosystems. *Ambio* **44**, 194–203 (2015).
290. Strauss, S. Y., Lau, J. A., Schoener, T. W. & Tiffin, P. Evolution in ecological field experiments: implications for effect size. *Ecol. Lett.* **11**, 199–207 (2008).
291. Lau, J. A., Peiffer, J., Reich, P. B. & Tiffin, P. Transgenerational effects of global environmental change: long-term CO₂ and nitrogen treatments influence offspring growth response to elevated CO₂. *Oecologia* **158**, 141–150 (2008).
292. O'Brien, M., Costa, D. & Servilla, M. Ensuring the quality of data packages in the LTER network data management system. *Ecol. Inform.* **36**, 237–246 (2016).
293. Porter, J. H. Evaluating a thesaurus for discovery of ecological data. *Ecol. Inform.* **51**, 151–156 (2019).
294. Vanderbilt, K. L. *et al.* A multilingual metadata catalog for the ILTER: Issues and approaches. *Ecol. Inform.* **5**, 187–193 (2010).

295. Servilla, M., Brunt, J., Costa, D., McGann, J. & Waide, R. The contribution and reuse of LTER data in the Provenance Aware Synthesis Tracking Architecture (PASTA) data repository. *Ecol. Inform.* **36**, 247–258 (2016).
296. National Science Foundation. *Long-Term Ecological Research Program: A Report of the 30-year Review Committee*. (2011).
297. LTER Information Management Committee Terms of Reference. (2011). Available at: https://im.lternet.edu/sites/im.lternet.edu/files/ToR_IMC_v1.pdf.
298. Jones, J. A. *et al.* Ecosystem Processes and Human Influences Regulate Streamflow Response to Climate Change at Long-Term Ecological Research Sites. *BioScience* **62**, 390–404 (2012).
299. Sharma, S. *et al.* A global database of lake surface temperatures collected by in situ and satellite methods from 1985–2009. *Sci. Data* **2**, 1–19 (2015).
300. Soranno, P. A. *et al.* Building a multi-scaled geospatial temporal ecology database from disparate data sources: fostering open science and data reuse. *GigaScience* **4**, 28 (2015).
301. Hampton, S. E. *et al.* Ecology under lake ice. *Ecol. Lett.* **20**, 98–111 (2017).
302. Wilcox, K. R. *et al.* Asynchrony among local communities stabilises ecosystem function of metacommunities. *Ecol. Lett.* **20**, 1534–1545 (2017).
303. Wilkinson, M. D. *et al.* The FAIR Guiding Principles for scientific data management and stewardship. *Sci. Data* **3**, 160018 (2016).
304. Stall, S. *et al.* Enabling FAIR Data Across the Earth and Space Sciences. *EOS* (2017).
305. FAIR data principles adopting signatories. Available at: <https://copdess.org/enabling-fair-data-project/commitment-statement-in-the-earth-space-and-environmental-sciences/signatories/>.
306. Hampton, S. *et al.* Big data and the future of ecology. *Front. Ecol. Environ.* **11**, 156–162 (2013).
307. Environmental Information Management Conference, 2008. Available at: <https://eim.ecoinformatics.org/eim2008>.
308. Environmental Information Management Conference, 2011. Available at: <https://eim.ecoinformatics.org/eim2011>.
309. Vanderbilt, K. & Gaiser, E. The International Long Term Ecological Research Network: a platform for collaboration. *Ecosphere* **8**, e01697 (2017).
310. Porter, J. *et al.* Wireless Sensor Networks for Ecology. *BioScience* **55**, 561–572 (2005).
311. Campbell, J. L. *et al.* Quantity is Nothing without Quality: Automated QA/QC for Streaming Environmental Sensor Data. (2013). doi:10.1525/bio.2013.63.7.10