

Long-Term Ecological Research on Ecosystem Responses to Climate Change

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In this article marking the 40th anniversary of the US National Science Foundation's Long Term Ecological Research (LTER) Network, we describe how a long-term ecological research perspective facilitates insights into an ecosystem's response to climate change. At all 28 LTER sites, from the Arctic to Antarctica, air temperature and moisture variability have increased since 1930, with increased disturbance frequency and severity and unprecedented disturbance types. LTER research documents the responses to these changes, including altered primary production, enhanced cycling of organic and inorganic matter, and changes in populations and communities. Although some responses are shared among diverse ecosystems, most are unique, involving region-specific drivers of change, interactions among multiple climate change drivers, and interactions with other human activities. Ecosystem responses to climate change are just beginning to emerge, and as climate change accelerates, long-term ecological research is crucial to understand, mitigate, and adapt to ecosystem responses to climate change.

Keywords: environmental forcing, extreme climate events, LTER Network, US National Science Foundation, human activities, ecosystem services

Accelerating climate change, including extreme climate events, has intensified the need to understand the response across ecosystems. This special issue marks the 40th anniversary of the US National Science Foundation's Long Term Ecological Research (LTER) Network. Although the LTER research agenda and sites were not explicitly designed to address climate change, the LTER program offers sustained ecological research among diverse ecosystems undergoing climate change. In this article, we demonstrate how a long-term ecosystem perspective emerging from four decades of LTER research provides key insights about ecosystem responses to climate change.

Long-term ecological research applies ecological principles over scales of time and space great enough to evaluate long-term change (Callahan 1984, Waide and Kingsland 2021). Since its inception in 1980, LTER has addressed major environmental issues based on cross-site comparative research, producing broadly applicable ecological principles (Franklin et al. 1990). The decade-to-century life span of LTER permits identification of the complex nature of temporal change, as well as spatial patterns of change (Hobbie et al. 2003). Long-term ecological research also addresses environmental stewardship, including policy, management, and conservation (Driscoll et al. 2012). The sustained nature of LTER research communities enhances the impacts of

science on environmental policy relative to short-term studies (Hughes et al. 2017). The commitment of the LTER community to serve broad public interests, and the LTER culture of openness, dispersed leadership, and partnership with policymakers and resource managers has been key to advancing basic science that supports the societal need to address major environmental challenges (Swanson et al. 2021). LTER research addresses environmental change in a human-dominated world (Robertson et al. 2012).

Four decades of LTER research have solidified three elements of a long-term ecosystem perspective: the invisible present, the invisible place, and spatiotemporal disturbance dynamics. The invisible present is the time scale “within which our responsibilities for planet Earth are most evident, [encompassing] our lifetimes and the lifetimes of our children and our grandchildren” (Magnuson 1990). Sustained long-term research places events or changes in their broader context and reveals lagged and cascading effects through time (Magnuson 1990). LTER research has demonstrated how legacies of human activities and natural events continue to influence ecosystems for decades and even centuries (Foster et al. 2003). With 40 years of record, augmented by pre-LTER data (Jones and Nelson 2021), the time frame of LTER research is now long enough to begin to distinguish responses to long-term climate change from

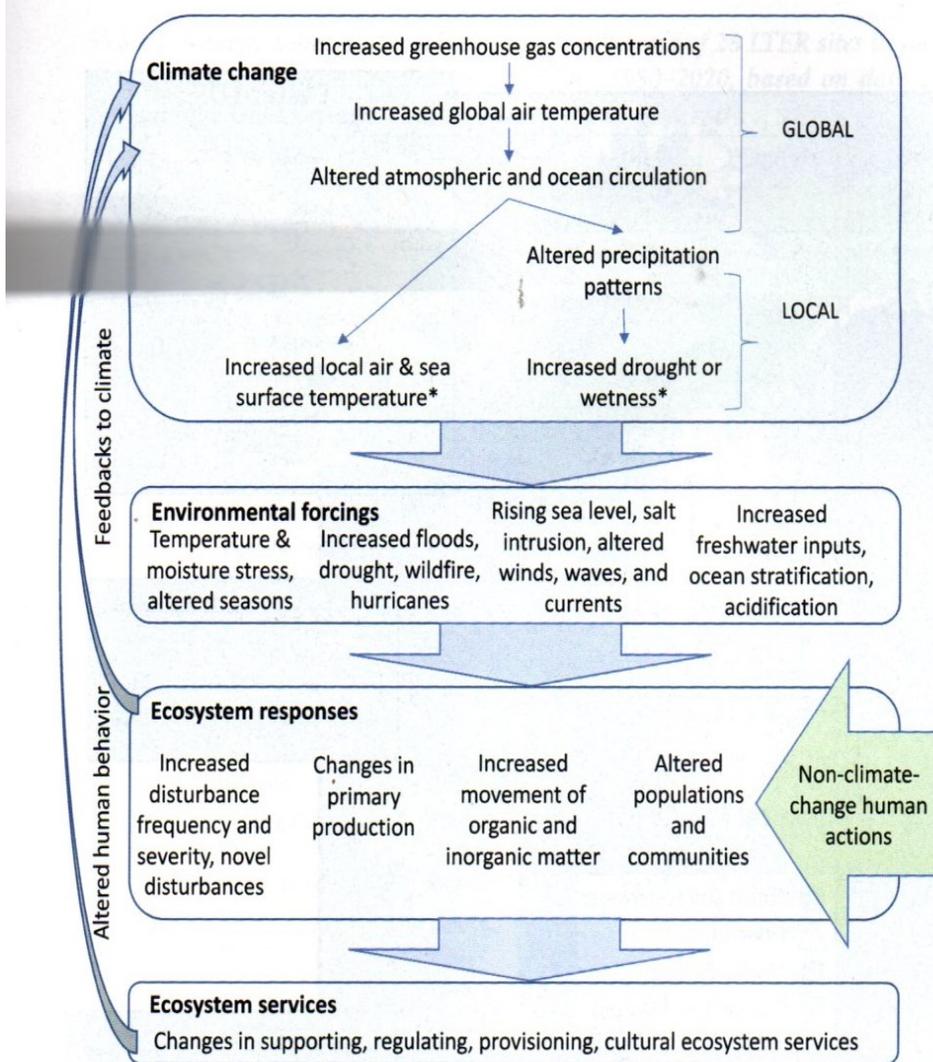


Figure 1. Conceptual diagram depicting climate change effects on ecosystem processes at LTER sites addressed in this article and special issue. Global climate change alters local temperature and moisture (*), producing varied types of environmental forcing. Ecosystem processes respond to environmental forcing and to non-climate-change human actions, and these responses affect ecosystem services. Both responses and ecosystem services feed back to climate change.

short-term or cyclical variation (e.g., Bahlai et al. 2021, Magnuson 2021).

The invisible place, by analogy, is the spatial scale within which events and ecosystem processes operate. It addresses how events and processes are influenced by their location along flow paths of matter and energy through landscapes and seascapes (Swanson and Sparks 1990). Examination of the ecological effects of global climate change requires multiscale research that uses knowledge of coarser scales of resolution to provide context for interpretation of fine-scale system behavior and knowledge of finer-scale processes to explain the mechanisms of patterns observed at coarser scales (Swanson and Sparks 1990). With 28 sites ranging from the Arctic and Antarctic to the tropics, the spatial extent of LTER research can connect site-level ecosystem responses to regionally varying climate change processes.

Long-term ecological research also contributes to understanding the temporal and spatial contexts of disturbance. The LTER program encompasses many ecosystem types

subject to multiple disturbances, documents slow or infrequent events, and provides a long-term baseline against which to detect change and measure ecosystem responses (Turner et al. 2003). LTER research examines how environmental drivers of disturbance act on ecosystem properties via specific mechanisms (Peters et al. 2011). LTER studies can identify disturbance mechanisms (specific stressors such as heat, impact force, abrasion, and burial that damage or kill organisms) associated with various disturbance types (phenomena such as fire, flood, wind, and wave action; Dale et al. 2005). With 28 sites and more than 900 site years of study, LTER research may detect how climate change is altering disturbance regimes and ecosystem responses (Gaiser et al. 2020).

Entering its fifth decade, LTER research now plays a vital role in deepening our understanding of ecosystem responses to climate change. This special issue evaluates 40 years of LTER research on climate change effects on ecosystems and suggests how LTER findings and approaches may guide continued research and policy in the coming decades. The 28 LTER sites are being subjected to varied types of environmental forcing from climate change, as well as other human activities that collectively affect a suite of ecosystem processes and ecosystem services, and ultimately, climate change itself (figure 1). LTER sites sample diverse ecosystems (figure 2) that are being subjected to

varying types and rates of climate change (Hayhoe et al. 2018, IPCC 2021). The core research areas of LTER—disturbance, primary production, cycling of organic and inorganic matter, and dynamics of populations and communities—permit comparison of ecosystem responses among sites. Therefore, our specific objectives in the present article are to describe and apply a conceptual framework for ecosystem responses to climate change that arises from a long-term ecosystem perspective; to describe how ecosystem responses to climate change vary among ecosystem types, their climatic and geographic settings, and ecosystem processes, based on findings and perspectives from LTER research; and to propose LTER synthesis and outreach efforts to address ecosystem responses to climate change.

Conceptual framing

The articles in this special issue consider a set of linked processes, including climatic forcing, environmental forcing, ecosystem response, feedback loops to the climate system,

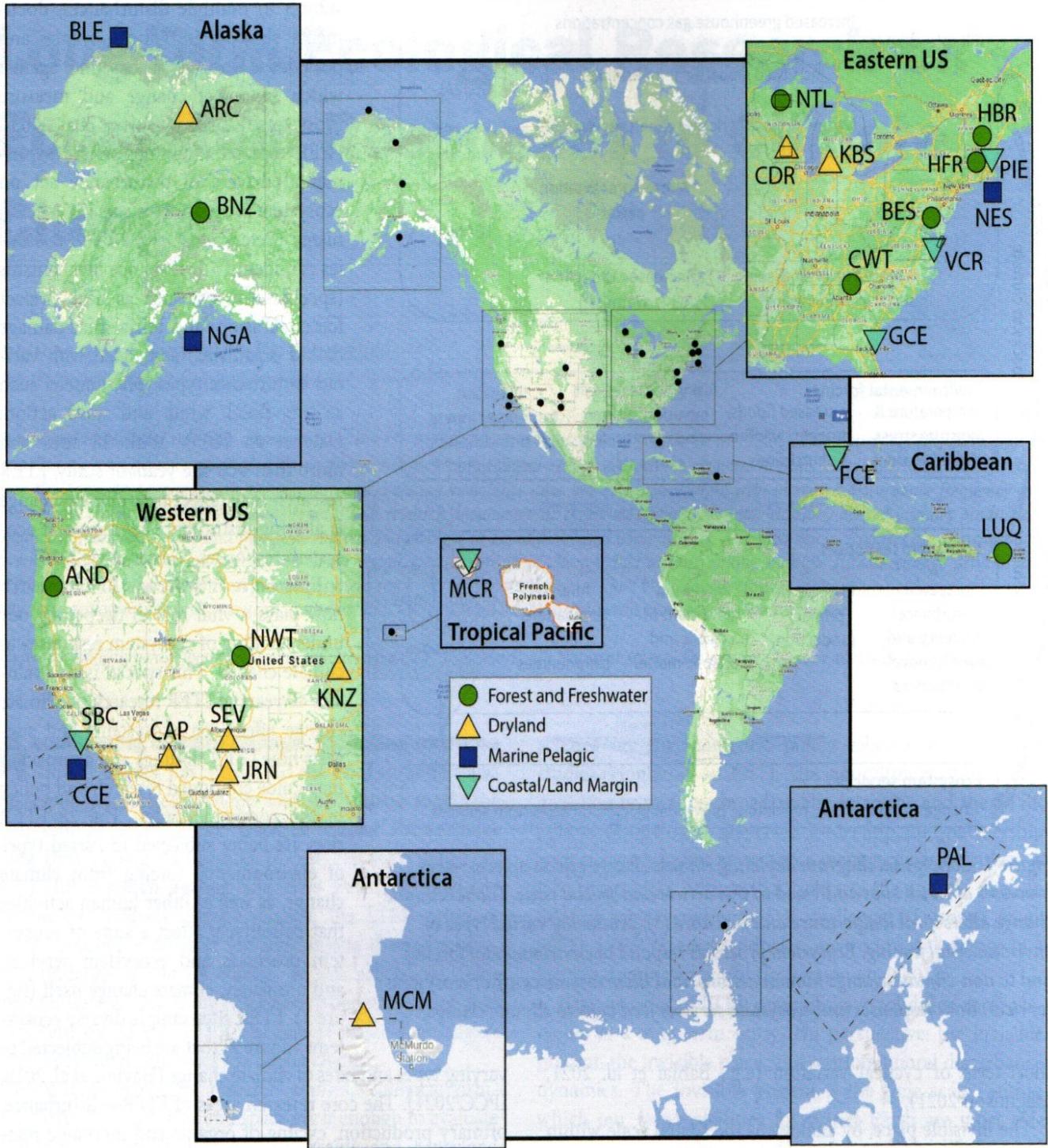


Figure 2. Locations of sites in the US Long-Term Ecological Research network, as of 2020, coded by group used in this special issue: marine pelagic, coastal, dryland, forest and freshwater.

and ecosystem services (figure 1). Increased concentrations of greenhouse gases are altering global temperature and atmospheric circulation, producing local changes in temperature and moisture. These processes result in environmental forcings that affect ecosystems, such as temperature and moisture stress; altered growing seasons and shorter winters; increased floods, drought, wildfire, and hurricanes; rising sea level, salt-water intrusion; altered winds, waves, and currents; increased freshwater inputs to oceans; and enhanced ocean stratification and acidification. Environmental forcings alter disturbance, primary production, cycling of organic and inorganic matter,

and population and community dynamics, and these changes can feed back to the climate system. Ecosystem processes are simultaneously responding to non-climate-related human actions, such as air pollution, land management, fishing, and introduced species. Collectively, these changes affect ecosystem services that shape human livelihoods, well-being, and survival and alter human behaviors in ways that feed back to affect climate change (Collins et al. 2011).

In the articles in this special issue, the 28 LTER sites active in 2019 were placed into one of four groups: forest and freshwater ($n = 9$), dryland ($n = 8$), coastal ($n = 6$), and marine

Table 1. Names, abbreviations, locations, and biomes of 28 LTER sites in four groups of ecosystems, and mean annual temperature and mean annual precipitation, 1950–2020, based on data from nearest site in the Global Historical Climatology Data network (see the supplemental material).

Group	Site name	Abbreviation	Latitude	Longitude	MAT (in degrees Celsius)	MAP (in millimeters)	Biome
Coastal	Florida Coastal Everglades	FCE	25.47	-80.85	24.0	1422	Freshwater marsh and estuary
	Georgia Coastal Ecosystem	GCE	31.43	-81.37	19.7	1262	Salt marsh and estuary
	Moorea Coral Reef	MCR	-17.49	-149.83	26.4	1363	Coral reef
	Plum Island Ecosystem	PIE	42.76	-70.89	9.7	1154	Estuary
	Santa Barbara Coastal	SBC	34.41	-119.84	15.1	414	Semi-arid coastal and marine
	Virginia Coast Reserve	VCR	37.28	-75.91	14.6	1131	Barrier island and lagoon
Dryland	Arctic	ARC	68.63	-149.61	-5.2	344	Arctic tundra
	Central Arizona–Phoenix	CAP	33.43	-111.93	20.2	382	Urban ecosystem
	Cedar Creek	CDR	45.40	-93.20	5.7	743	Savanna and tallgrass prairie
	Jornada	JRN	32.62	-106.74	14.7	243	Desert
	Kellogg Biological Station	KBS	42.40	-85.40	9.6	943	Row crop agriculture
	Konza Prairie	KNZ	39.09	-96.58	12.8	877	Tallgrass prairie
	McMurdo Dry Valleys	MCM	-77.00	162.52	-17.3	171	Polar desert
	Sevilleleta	SEV	34.35	-106.88	13.6	210	Desert and grassland
	Andrews Forest	AND	44.21	-122.26	9.1	1873	Coniferous forest
Forest and freshwater	Baltimore Ecosystem Study	BES	39.10	-76.30	13.1	1087	Urban ecosystem
	Bonanza Creek	BNZ	64.86	-147.85	-2.2	320	Taiga
	Coweeta	CWT	35.06	-83.43	12.9	1796	Deciduous forest
	Hubbard Brook	HBR	43.94	-71.75	6.0	989	Deciduous forest
	Harvard Forest	HFR	42.53	-72.19	7.8	1140	Deciduous forest
	Luquillo	LUQ	18.30	-65.80	25.2	2838	Tropical rainforest
	North Temperate Lakes	NTL	46.01	-89.67	4.3	824	Temperate lake
	Niwot Ridge	NWT	39.99	-105.38	-0.5	499	Alpine tundra
	Beaufort Lagoon Ecosystem ^a	BLE	71.29	-156.79	-11.6	128	Estuary
	California Current Ecosystem	CCE	32.87	-120.28	15.1	414	Marine
Marine pelagic	Northeast US Shelf	NES	40.70	-70.88	10.3	1172	Marine
	Northern Gulf of Alaska	NGA	59.05	-148.70	4.5	1707	Subarctic marine
	Palmer Antarctica	PAL	-64.77	-63.06	-5.1	473	Polar marine

Abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature.

^aBeaufort Lagoon is a shallow sea ice-dominated coastal marine LTER.

pelagic ($n = 5$) ecosystems. Each group encompasses varied geographic and climate settings (table 1, figures 2 and 3, supplemental figure S7). Forests are ecologically and physically connected to freshwater ecosystems through surface and groundwater flows, and the forest and freshwater LTER

group includes boreal, temperate, and tropical forests and associated streams and lakes, all spanning tropical to sub-Arctic latitudes. Drylands encompass nonforested terrestrial ecosystems with higher ratios of temperature to precipitation indicating greater moisture stress than forest and freshwater

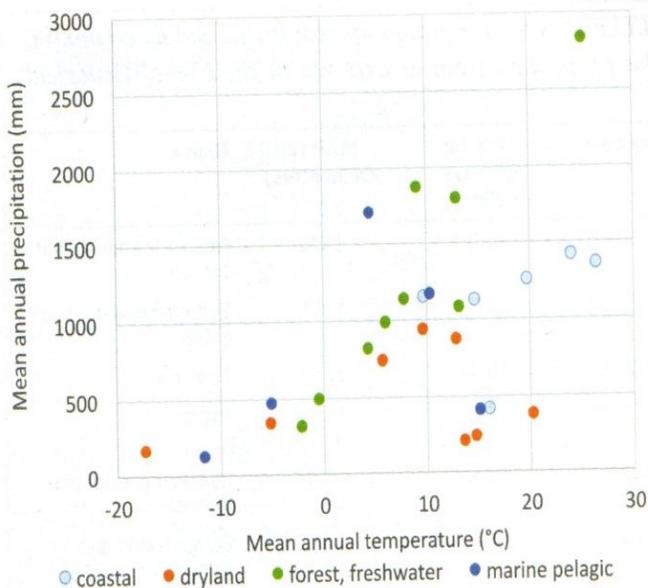


Figure 3. Mean annual air temperature and mean annual precipitation by ecosystem type at 28 LTER sites, based on data from the Global Historical Climatology Network site nearest to each LTER site (see the supplemental material for details of data sets and analyses). See table 1 for data and site names.

LTER sites (figure 3). The dryland LTER group includes hot deserts, cold deserts, tundra, tallgrass prairie, and row crops, all spanning subtropical to polar latitudes. Coastal LTER sites are ecosystems at land margins, where terrestrial processes and freshwater interact with the ocean and oceanographic processes. Ecosystems in the coastal LTER group include barrier islands, seagrass meadows, mangrove forests, salt marshes, coral reefs, and kelp forests, all spanning tropical to temperate latitudes. Marine pelagic LTER sites are ocean ecosystems along continental margins, where processes within the water column are influenced by proximity to the coasts and by deep water beyond continental shelves. The marine pelagic LTER group includes ecosystems with a wide range of terrestrial influences spanning tropical to polar latitudes. Each group represents diverse ecosystem types located across the Western Hemisphere (figure 2) encompassing wide ranges in mean annual precipitation and mean annual temperature (figure 3). Collectively these 28 LTER sites provide unique opportunities for broadscale synthesis. But the LTER network is much more than a collection of sites: It is an open, interactive, diverse community of researchers committed to mechanistic research, synthesis of findings, and collaboration with policymakers (Driscoll et al. 2012, Swanson et al. 2021).

Climate change at LTER sites

Climate change affects environmental forcing and ecosystem responses through changes in average and extreme temperature and moisture on multiple time scales. We quantified change in air and sea surface temperature and moisture at LTER sites by ecosystem group and geographic setting, for four time periods (1980–2020 versus the twentieth century,

1930–2020, 1950–2020, and 1980–2020) using global gridded data sets (see the supplemental material).

Most LTER sites warmed 0.3 to 0.4 degrees Celsius per decade from 1980 to 2020, and the rates of warming were lowest at tropical LTER sites and highest at polar LTER sites (figure 4, supplemental table S4). Of the 22 LTER sites with Standardized Precipitation–Evaporation Index data (see the supplemental material), 14 became functionally wetter (LTER sites in the Arctic, the eastern United States, and Puerto Rico), whereas 8 became functionally drier (LTER sites in the southwest United States) from 1980 to 2020 (figure 5). The rate of warming has accelerated at almost all LTER sites over the LTER period (1980–2020) relative to the twentieth century. Most LTER sites warmed at rates two to three times faster in 1980 to 2020 than in 1930 to 2020, and the warming rates increased by three to ten times at six LTER sites (figure 6, table S4).

Changes in extremes and warming rates provide different perspectives of climate change effects on LTER ecosystems. Absolute change, measured in degrees Celsius, indicates change in heat energy to the ecosystem, whereas relative warming, measured in percentiles, can indicate changes in extremes, such as the hottest and coldest conditions. Some LTER sites, especially at subtropical and tropical latitudes, are not warming very fast in absolute terms, but the number of extreme hot months from 1980 to 2020 was three to four times higher than it was in the twentieth century (figure 7, supplemental table S5, supplemental figure S3). Other LTER sites, especially at subpolar latitudes, are warming rapidly in absolute terms but have lesser increases in extreme hot months (figure 7, table S5).

The increase in extreme hot months and the corresponding loss of extreme cold months has accelerated during the LTER period (1980–2020). By the 2000s, the frequencies of extreme hot and cold months were outside the range of variation from the 1930s to the 1970s at almost all LTER sites: The frequency of extreme hot months more than tripled at five of six coastal LTER sites, four of five marine pelagic LTER sites, three of eight dryland LTER sites, and two of nine forest and freshwater LTER sites, with a corresponding loss of extreme cold months (figure 8). Wetness and dryness extremes also have become more frequent since 2000 but at fewer sites. Extreme wet months were more frequent in the 2000s or 2010s than in the 1930s through the 1970s at three of nine forest and freshwater LTER sites (Hubbard Brook, Luquillo, North Temperate Lakes) and two of eight dryland LTER sites (Cedar Creek, Kellogg Biological Station), whereas extreme dry months were more frequent at four dryland LTER sites (Arctic, Central Arizona–Phoenix, Jornada, Sevilleta; figure 9). Both wet and dry extremes have increased at some LTER sites (e.g., Luquillo).

Trends in temperature and wetness or dryness varied by season and location, with rapid warming at LTER sites in the austral fall and winter in Antarctica; in fall and winter in Alaska; in spring, summer, and fall in the continental United

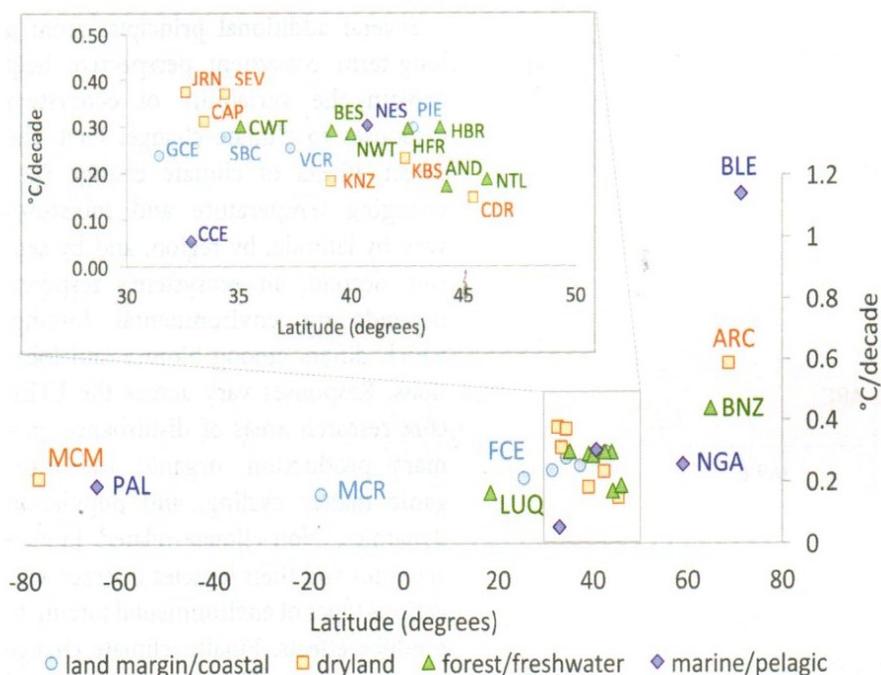


Figure 4. Rates of change in temperature from 1980 to 2020 based on Goddard Institute for Space Studies air and sea surface temperature anomalies for LTER sites, by latitude (see the supplemental material for details of data sets and analyses).

States; and year-round in the tropics (supplemental table S6, supplemental figure S5) and with drier winter and spring at LTER sites in Alaska, the Rocky Mountains, and the southwestern United States and wetter autumn at LTER sites in the north central and northeastern United States (supplemental table S7, supplemental figure S6).

Environmental forcing and human activities

LTER sites are being exposed to many types of local environmental forcing driven by climate change, as is described in the articles in this special issue (figure 1). Heat waves have imposed temperature stress on all ecosystem types. Drought has exacerbated moisture stress and wildfire in some forest and freshwater and dryland ecosystems. The loss of ice, snow, and permafrost is altering runoff patterns; increasing flooding in forest, freshwater, and dryland ecosystems; and augmenting freshwater delivery to some marine pelagic ecosystems. Altered winds, waves, and increased hurricanes compounded by sea level rise and saltwater intrusion are affecting coastal ecosystems, whereas currents and upwelling patterns are changing in coastal and marine pelagic ecosystems. Ocean ecosystems are experiencing stronger stratification and acidification.

Environmental forcing from climate change (figure 1) differs among the four ecosystem types and by location. In forest and freshwater systems, climate change melts snow and ice, thaws permafrost, and alters precipitation (Campbell et al. 2022, this issue). Extreme heat and increased evaporative demand impose temperature and moisture stress. Forest and freshwater sites in the eastern United States and the tropics have experienced increases in storm intensity, including

more frequent and intense hurricanes, floods, and ice storms, whereas those in the western United States and Alaska have experienced increased dry conditions and wildfire (figure 1).

In dryland ecosystems, climate change increases temperature and moisture stress, flooding, and wind erosion (Hudson et al. 2022, this issue). Heat waves and reduced humidity accentuate moisture stress. Increased precipitation and flooding have affected dryland systems in the central and north central United States, whereas increased wet-dry extremes have intensified flooding, drought, erosion, and dust transport in southwestern deserts. At the Arctic tundra LTER, the air has become warmer and drier, increasing climatic drought and even wildfire, and permafrost thaw has simultaneously increased streamflow (figure 1).

In coastal systems, climate change contributes to temperature stress, altered wind and waves, and saltwater intrusion (Reed et al. 2022, this issue). Reduced coastal upwelling, ocean acidification, and other biogeochemical changes in soil, sediment, and water are affecting coastal ecosystems. Less frequent freezing events, increased marine heat waves, and reduced vertical ocean mixing impose temperature stress. Rising sea levels have increased inundation and saltwater intrusion. Coastal ecosystems have experienced increased extreme waves and wind, higher storm surges, and coastal erosion, as well as increased flooding and drought (figure 1).

In marine pelagic systems, climate change contributes to changes in water circulation, warming, and effects on sea ice (Ducklow et al. 2022, this issue). Circulation and mixing effects include reduced upwelling, increased stratification due to changing temperature and salinity and decreased vertical mixing. Marine heat waves have imposed temperature stress at all latitudes. In Arctic and Antarctic latitudes, melt and retreat of glaciers increase freshwater inputs. Higher sea surface and air temperature and evaporation increase precipitation (rain or snow). Sea ice changes include later advance and earlier retreat of seasonal ice and reduced ice duration (figure 1).

Non-climate-related human activities interact with environmental forcing from climate change to influence ecosystem responses (figure 1, supplemental table S3). Marine pelagic LTER sites have been affected by fishing, whaling and the cessation of whaling, and, more recently, by microplastics. In coastal LTER sites, fishing and marine mammal extirpation have altered community composition, whereas urbanization and coastal development have altered water, sediment, and nutrient dynamics. Dryland LTER sites have

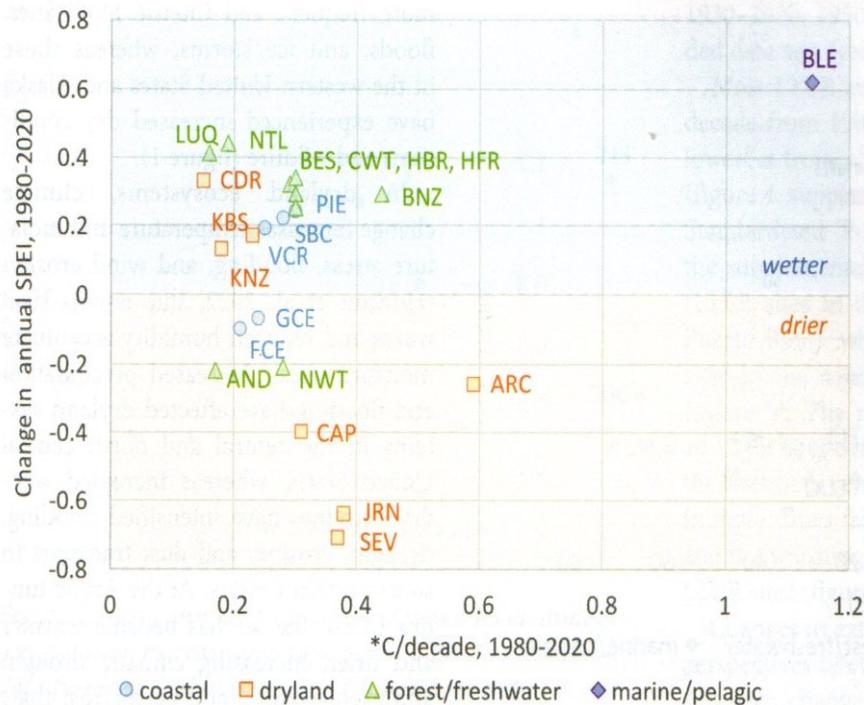


Figure 5. Controlling for temperature change, over the LTER period (1980 to 2020), some LTER sites are becoming functionally wetter, whereas others are becoming functionally drier, based on the Standardized Precipitation–Evaporation Index (SPEI; see the supplemental material for details of data and analyses). SPEI data are not calculated for open ocean sites or Antarctic sites (CCE, NES, NGA, MCM, MCR, or PAL). Excluding the Alaska sites, which are all warming faster than the continental US or Puerto Rico, warming rates are higher at sites that have become drier and lower at sites that have become wetter.

been affected by clearing, agriculture, and field abandonment; the extirpation of native grazers and the introduction of domestic grazers; diversion of water; elevated atmospheric deposition and ozone; and urbanization and exurban development. Forest and freshwater LTER sites have been altered by forest clearing, agriculture, grazing, and field abandonment; logging and road construction; fire suppression; elevated nitrogen and sulfur deposition and ozone; introduced species and plant pathogens; and urbanization and exurban development.

Ecosystem responses to climate change

The ecosystem responses to climate change at LTER sites are extremely varied and, in many cases, just emerging. As is demonstrated in the articles in this special issue, a long-term ecosystem perspective offers important insights into how ecosystems are responding to changing climate. A few simple principles emerge, but for the most part, ecosystem responses are highly individualistic. Responses are most evident at ecosystems exposed to the most rapid rates of change or experiencing the most severe climate-related disturbances. Moreover, ecosystem responses can be most clearly linked to climate change where warming has led to a phase transition of water from ice to liquid water or to water vapor. Beyond these, the responses to climate change are quite variable among ecosystems.

Several additional principles from a long-term ecosystem perspective help explain the variability of ecosystem responses to climate change. First, the direct effects of climate change (i.e., changing temperature and moisture) vary by latitude, by region, and by season. Second, an ecosystem's response depends on environmental forcing, which differs among biomes and locations. Responses vary across the LTER core research areas of disturbance, primary production, organic and inorganic matter cycling, and population dynamics. Non-climate-related human activities and their legacies interact with various types of environmental forcing to produce effects. Finally, climate change results in a cascade of interactions and legacies over time (the invisible present, disturbance cascades), and in space (the invisible place), which play out over decades to centuries. We briefly discuss these principles below. Examples are taken from the companion articles in this special issue and from articles accessible in publication lists linked at lternet.edu.

Responses are greatest where warming is most rapid. In general, across the 28 LTER sites, ecosystem responses to climate change are most prominent where the greatest increases in absolute temperature have occurred (i.e., high-latitude sites). For example, increased wildfire has altered ecosystem processes and communities in the boreal forest (Bonanza Creek) and tundra (Arctic) LTER sites, and changes in freshwater inflows, sediment, and light have affected a shallow sea ice-dominated coastal marine LTER (Beaufort Lagoon Ecosystem). Ecosystem responses also are evident at subtropical or tropical sites, which have experienced the greatest relative increases in temperature. Increased hurricanes and heat waves have altered ecosystem processes in tropical rainforest (Luquillo) and in a tropical coral reef (Moorea).

Responses are notable where ice is melting. Many ecosystem responses to changing climate are associated with a threshold change in the phase of water. Liquid water alters energy exchange, transports nutrients and sediment, and enables growth and metabolism. In marine pelagic ecosystems, freshwater outflow from the melting Greenland icecap is increasing stratification of the Atlantic Ocean near New England (Northeast Shelf), permafrost thaw is promoting a shift to shrubs in the Alaskan tundra (Arctic), permafrost thaw and increased river discharge have altered processes in a shallow sea ice-dominated coastal marine ecosystem

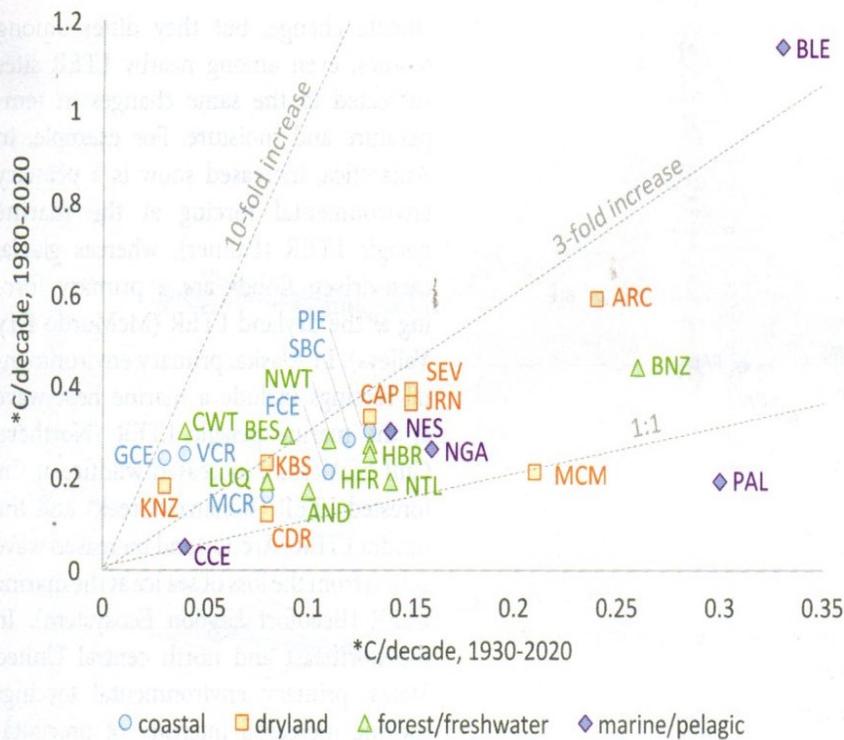


Figure 6. The rate of temperature change during the LTER period (1980 to 2020) has accelerated at almost all LTER sites compared to the rate from 1930 to 2020. Warming has accelerated by more than two times and up to ten times. Some sites with relatively low warming rates from 1930 to 2020 have experienced large acceleration in 1980 to 2020.

(Beaufort Lagoon), and a shift from snow to rain may be drowning penguin chicks in Antarctica (Palmer). In coastal ecosystems, reductions in freezing events have enabled mangroves to expand their northern range limit (Florida Coastal Everglades) and permitted native woody species to expand seaward (Virginia Coastal Reserve). In forest and freshwater ecosystems, a shift from snow to rain has altered plant function and streamflow (Baltimore, Hubbard Brook, Harvard Forest) and increased stream water phosphorus inputs and algal blooms (North Temperate Lakes), whereas permafrost thaw has expanded shrub cover in alpine tundra (Niwot Ridge). In drylands, permafrost thaw has increased transport of organic and inorganic material to lakes in the tundra (Arctic), the loss of snowpack has increased greenhouse gas emissions (Kellogg), and a glacial melt outburst flood altered stream and lake ecosystems in Antarctica (McMurdo Dry Valleys). A shift in the phase of water from liquid to vapor (i.e., increased evaporation) also is linked to increased dust transport in the US Southwest (Central Arizona–Phoenix), reduced primary production in deserts (Jornada), and increased wildfire in Alaska (Bonanza) and the US Pacific Northwest (Andrews).

Responses vary by core research area. Ecosystem responses to climate change are evident in all core research areas of LTER designated at the inception of the program: disturbance, primary production, cycling of organic and inorganic matter, and populations and communities, but the responses differ among the core research areas (figure 1). Most LTER sites

report increases in the frequency and severity of disturbance events associated with climate change, and many sites have been exposed to unprecedented types of disturbance. Altered disturbances include increased frequency and severity of terrestrial and marine heat waves, tropical cyclones, flooding, ice storms, and larger and more severe wildfires.

Changes in primary production also are being observed at LTER sites. Increased intensity of weather events involving heat, drought, wind, waves, floods, or wildfire are associated with losses but also some gains in live biomass in forest, dryland, coastal, and marine pelagic ecosystems. Net primary production has increased in some ecosystems because of a loss of sea ice, snow, and glaciers, and it has declined in other ecosystems because of a variety of mechanisms including combustion, physical abrasion, heat stress, moisture stress, defoliation, wave action, and the loss of light from burial or suspended sediment.

Movement and storage of organic matter also have been altered by climate

change at many LTER sites. Changes include remineralization of buried carbon in seagrass meadows as a result of marine heat waves (Georgia Coastal), peat collapse in salt marshes due to saltwater intrusion (Florida Coastal Everglades), losses due to wildfire (Arctic, Andrews), increased decomposition of soil organic matter (Harvard Forest), increased dissolved organic matter delivery to streams and lakes in part due to increased temperature and runoff (Hubbard Brook), and altered carbon fixation and export to the deep ocean due to sea surface warming (California Current, Northern Gulf of Alaska).

Changes in temperature, precipitation intensity, and phase of water have altered transport of inorganic material at some LTER sites. Some changes increase transport. Thawing permafrost increased the available pool of nitrogen in the boreal forest (Bonanza), hurricanes have produced pulses of nitrate and potassium in a tropical rain forest (Luquillo), and extreme precipitation events have augmented nutrient inputs to lakes (North Temperate Lakes). In contrast, other changes decrease transport of inorganic material. Increased soil carbon has reduced nitrogen availability in a temperate deciduous forest (Hubbard Brook). Increased freshwater inputs to marine pelagic systems may reduce salinity because of dilution (Northeast Shelf) and sea surface warming can suppress upwelling and delivery of inorganic material (California Current).

Populations and communities at LTER sites are responding to climate change, but many of these effects also are attributable to non-climate-change related human activities (see below). Examples of direct effects of climate

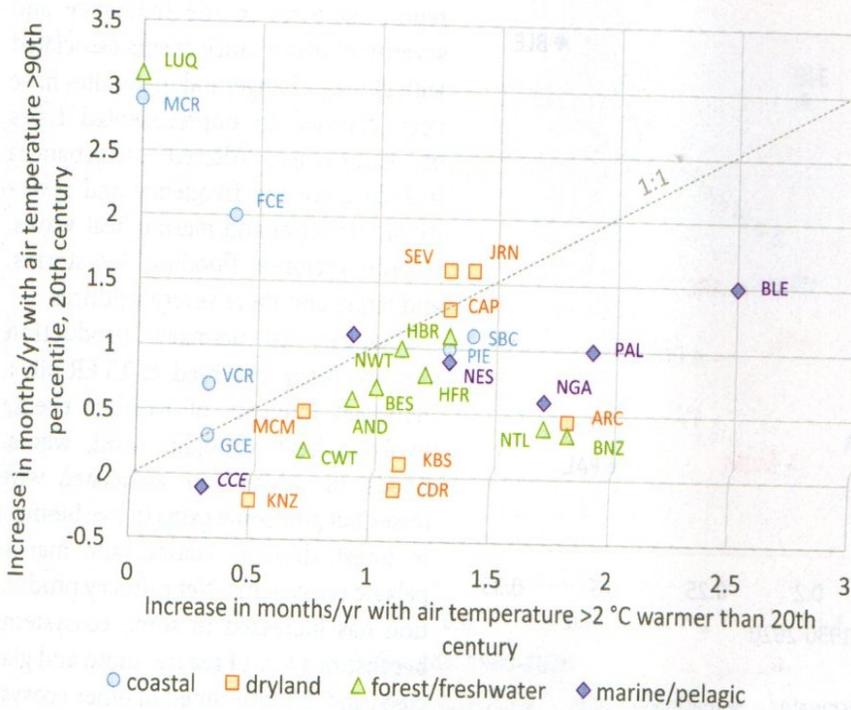


Figure 7. Extremes of temperature became more frequent at LTER sites during the LTER period (1980 to 2020) both in absolute terms (increase in months per year with air temperature more than 2 degrees Celsius warmer than in the twentieth century, x-axis) and relative terms (increase in months per year with air temperature above the 90th percentile, twentieth century, y-axis). Some LTER sites with little increase in absolute extremes had large increases in relative extremes (e.g., FCE, LUQ, MCR), and vice versa (e.g., ARC, BLE, BNZ, CDR, KBS, NGA, NTL, PAL).

change on populations are few but include declines in cold water dependent fish species and increased cyanobacteria that drive harmful algal blooms (North Temperate Lakes), reductions in seabird (Adélie penguin) populations possibly in response to changes in snow (Palmer Antarctic), and changes in fish species abundance in kelp forests (Santa Barbara Coastal).

Responses vary depending on climate change drivers. The diverse ecosystem types represented by LTER sites are being subjected to different combinations of increased temperature and changes in moisture (figure 5), as well as different seasonal timings of these changes. Marine pelagic sites and coastal LTER sites respond to change in air and water temperatures and may respond to changes in moisture only indirectly through changes in terrestrial freshwater inputs. Some terrestrial LTER sites are becoming warmer and drier, whereas others are becoming warmer and wetter, and at one LTER (Arctic Tundra) the air is warming and drying, but permafrost thaw is producing wetter soils. Trends in temperature and moisture also differ by season among LTER sites, likely contributing to differential effects on seasonally driven ecological processes.

Responses vary with environmental forcing. Environmental forcings are the proximal drivers of ecosystem responses to

climate change, but they differ among biomes, even among nearby LTER sites subjected to the same changes in temperature and moisture. For example, in Antarctica, increased snow is a primary environmental forcing at the marine pelagic LTER (Palmer), whereas glacial melt-driven floods are a primary forcing at the dryland LTER (McMurdo Dry Valleys). In Alaska, primary environmental forcings include a marine heat wave at the marine pelagic LTER (Northern Gulf of Alaska), increased wildfire at the forested LTER (Bonanza Creek) and the tundra LTER (Arctic), and increased wave action from the loss of sea ice at the marine LTER (Beaufort Lagoon Ecosystem). In the northeast and north central United States, primary environmental forcings include increased intensity of precipitation in forest and freshwater LTER sites (Baltimore, Harvard Forest, Hubbard Brook, North Temperate Lakes) and some dryland LTER sites (Cedar Creek, Kellogg Biological Station), changes in ocean currents and freshwater mixing in the marine pelagic LTER (Northeast Shelf), and rising sea level and salt water intrusion at the coastal LTER (Plum Island).

Responses depend on other human activities. LTER research has demonstrated that ecosystem and ecological processes continue to respond to past human activities and other nonclimate disturbances for decades or centuries (Foster et al. 2003, Turner et al. 2003). The legacies of these past and ongoing human activities and other natural disturbances interact with climate change, producing diverging ecosystem responses even among LTER sites in similar biomes with similar environmental forcing. For example, among marine pelagic LTER sites, ecosystem responses to marine heat waves vary based on past and ongoing fisheries management, including krill harvests (Palmer Antarctic) and twentieth century fisheries collapse (Northeast Shelf, California Current Ecosystem, Northern Gulf of Alaska). Ecosystem responses to climate change at dryland LTER sites are mediated by past removal of native grazers and introduction of domestic cattle (Konza Prairie, Jornada). Responses in coastal LTER sites depend on adjacent local development (Santa Barbara Coastal), changes in river flow input due to upstream development (Georgia Coastal, Plum Island), and diversions of freshwater inputs (Florida Coastal Everglades). Ecosystem responses to climate change in forest and freshwater LTER sites are affected by diverse histories of logging (Andrews, Hubbard Brook), fire suppression (Coweeta), forest clearing and agriculture (Baltimore,

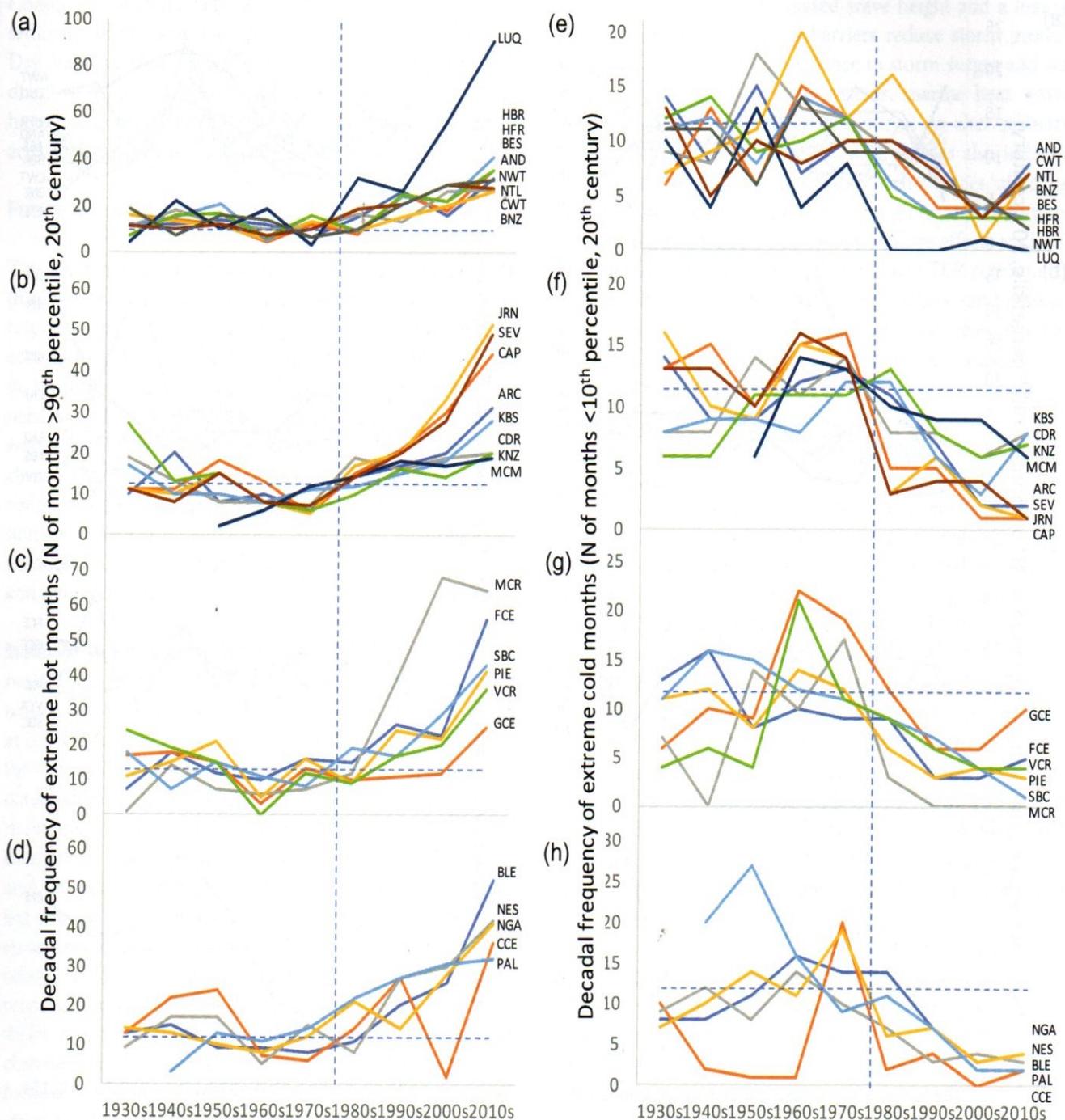


Figure 8. Decadal frequency of numbers of extreme hot months (a–d) and extreme cold months (e–h) in relative terms for LTER sites from the 1930s to 2010s, based on Goddard Institute for Space Studies air and sea surface temperature anomaly data (see the supplemental material for details of data sets and analyses). (a, e) forest and freshwater sites, (b, f) dryland sites, (c, g) coastal sites, (d, h) marine pelagic sites. Vertical dashed line indicates beginning of LTER period. Horizontal dashed line is the expected frequency of months per decade in the highest 90% and lowest 10% of the distribution for the twentieth century (i.e., 12 months per decade).

Luquillo), air pollution (Hubbard Brook, Niwot Ridge), and introduced pathogens (Coweeta, Harvard Forest). Human responses, such as salvage logging conducted in response to wildfire (Andrews) or forest mortality from insects (Harvard Forest), compound ecosystem responses to climate change. The 40-year history of LTER demonstrates the value of a long-term perspective that integrates multiple drivers of ecosystem response.

Insights from a long-term ecosystem perspective. A long-term ecosystem perspective provides insights into how climate change affects all aspects of populations, communities, and ecosystem processes and into how these effects cascade through time and space. The invisible present permits the comparison of responses to successive hurricane events as the record becomes longer at a tropical forest (Luquillo). It reveals lagged responses of wildfire and dust storms to changes in primary

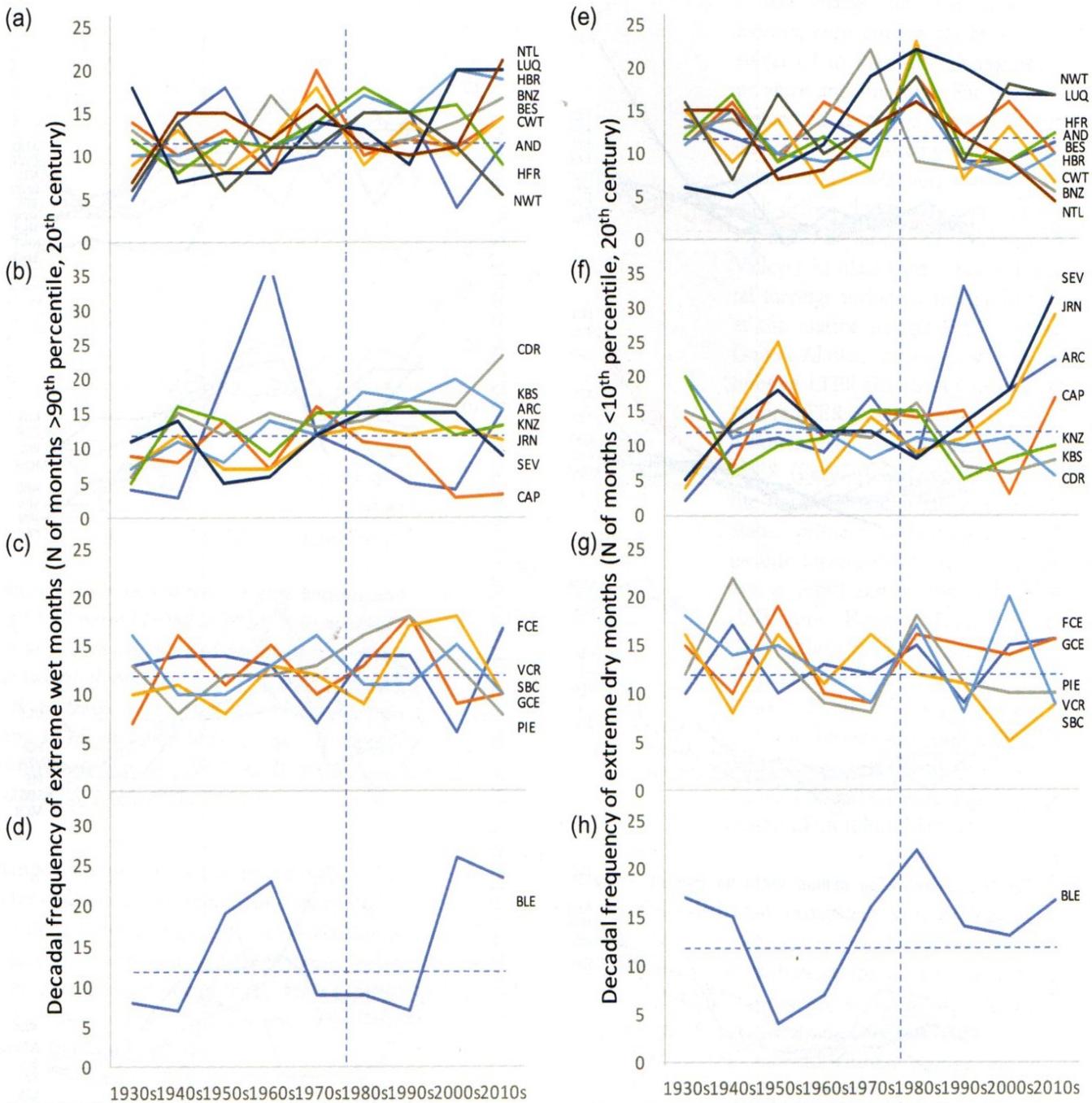


Figure 9. Decadal frequency of numbers of extreme wet months (a–d) and extreme dry months (e–h) in relative terms for LTER sites from the 1930s to 2010s, based on Standardized Precipitation–Evaporation Index (SPEI) data (see the supplemental material for details of data sets and analyses). (a, e) forest and freshwater sites, (b, f) dryland sites, (c, g) coastal sites, (d, h) marine pelagic sites. Vertical dashed line indicates beginning of LTER period. Horizontal dashed line is the expected frequency of months per decade in the highest 90% and lowest 10% of the distribution for the twentieth century (i.e., 12 months per decade). SPEI data do not exist for CCE, NES, NGA, MCM, MCR, or PAL.

production in US Southwest desert LTER sites (Jornada, Sevilleta, Central Arizona–Phoenix). But despite the many changes observed, so far, climate change is implicated in very few major shifts in ecosystem type or state at LTER sites. A long-term perspective can reveal ecosystem responses such as resilience to multiple disturbances (in coral reefs, Moorea; in tropical forest, Luquillo), slow succession (in boreal forest, Bonanza), or changing community composition with continued ecosystem function (in prairies, Konza and Cedar Creek;

in deserts, Jornada, Sevilleta; and in polar oceans, Palmer). A long-term ecosystem perspective also reveals the role of spatial location (the invisible place), such as how the location of lakes in the landscape affects their response to climate change (North Temperate Lakes) or how the position of a forest in the landscape affects its exposure to wildfire (Andrews). In addition, a long-term ecosystem perspective considers spatial and temporal cascades of disturbances, such as increased upwind storm intensity affecting defoliation of mangroves (Florida

Coastal Everglades) or glacial melt outburst flood delivery of sediment suppressing lake primary production (McMurdo Dry Valleys). Cascading effects of climate change through direct and indirect effects and non-climate-change related human actions are being observed at numerous LTER sites across various biomes (Bahlai et al. 2021).

Future work for LTER

This examination of ecosystem responses to climate change from 40 years of LTER research indicates that ecosystem responses to climate change are just emerging, differ among ecosystem types and locations, and are likely to accelerate in coming decades. These findings raise two key issues: a need for LTER to promote sustained and cross-site deliberation about how different ecosystems are responding to climate change and an imperative for LTER to promote environmental stewardship by engaging governmental agencies, nongovernmental organizations, land trusts, environmental managers, and other actors in dialogue about science, policy, and management.

Sustained long-term cross-LTER research. Crucial insights into major ecological principles about ecosystem responses to climate change require not only sustaining long-term research at individual sites but also creating and maintaining forums for cross-LTER synthesis, which are lacking. Such forums could address key questions that emerge from this overview, including the following: How do disturbance effects on ecosystems change as disturbances become more frequent and increase in intensity? In which ecosystems is increasing climate variability leading to state changes in ecosystem structure or function, and why? What forms of non-climate-related human activities mitigate or magnify ecosystem responses to climate change? Why do ecosystem responses differ among ecosystems subjected to the same or similar climate or environmental forcing? Although there are many forums to discuss climate change, there is no sustained effort to identify ecological principles governing ecosystem responses to climate change. A significant additional investment to create and sustain such fora, building on LTER, would provide a unique contribution to basic and applied science and provide an effective mechanism for the research community to interact with resource managers.

Ecosystem services and environmental stewardship. Climate change is altering ecosystem services at LTER sites, including sustaining, regulating, provisioning, and cultural services (figure 1). For example, increased drought, heat, and the associated disruption of soil biocrust formation may increase wind erosion and dust storms, damaging human health in US Southwest desert LTER sites. Increased precipitation is overwhelming flood protection capacities of some forest and freshwater LTER sites, whereas increased heat and more frequent disturbance, including wildfire, is reducing carbon storage in forest and tundra LTER sites.

In coastal ecosystems, increased wave height and a loss of coastal vegetation and sand barriers reduce storm protection capacity and coastal resilience to storm surges and sea level rise. In marine pelagic systems, marine heat waves and changes in upwelling may suppress or alter primary production, damaging fisheries. LTER studies also indicate that ecosystem responses alter ecosystem services, affecting human outcomes differently among regions and ecosystem types. Indeed, it appears that climate change effects are local and should be managed accordingly. The LTER community should actively collaborate with policymakers, land managers, and resource managers to promote locally relevant environmental stewardship in the face of climate change.

Conclusions

The 40th anniversary of the establishment of the US Long-Term Ecological Research Network provides an opportunity to ask what we have learned about ecosystem responses to climate change from long-term ecological research. Long-term ecological research provides an integrated perspective that permits linking changes in greenhouse gases to environmental forcing, ecosystem responses and their effects on ecosystem services and climate feedback loops. The syntheses of LTER research in this special issue indicate that virtually all ecosystem and ecological processes are being affected by changing climate but often differentially by region or ecosystem type. On the other hand, so far, climate change is implicated in very few major shifts in ecosystem type or state at LTER sites. Many other past and ongoing human activities continue to produce ecological change at LTER sites and most places on Earth, and those activities and their legacies interact with climate change over multiple decades to centuries.

The present article and the others in this special issue assess place-based LTER research in the context of anthropogenic climate change. Ecosystems are responding to changes in temperature, moisture, and environmental forcing that vary among regions and biomes. Ecosystem responses to climate change are just emerging, are extremely varied, and are likely to intensify as climate change accelerates. The observed ecosystem responses at US LTER sites and ongoing work at other sites and networks globally attest to the value of and need for continued long-term ecological research in order to understand, mitigate, and adapt to ecosystem responses to global climate change.

Supplemental material

Supplemental data are available at *BIOSCI* online.

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