Forest and Freshwater Ecosystem Responses to Climate Change and Variability at US LTER Sites

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Forest and freshwater ecosystems are tightly linked and together provide important ecosystem services, but climate change is affecting their species composition, structure, and function. Research at nine US Long Term Ecological Research sites reveals complex interactions and cascading effects of climate change, some of which feed back into the climate system. Air temperature has increased at all sites, and those in the Northeast have become wetter, whereas sites in the Northwest and Alaska have become slightly drier. These changes have altered streamflow and affected ecosystem processes, including primary production, carbon storage, water and nutrient cycling, and community dynamics. At some sites, the direct effects of climate change are the dominant driver altering ecosystems, whereas at other sites indirect effects or disturbances and stressors unrelated to climate change are more important. Long-term studies are critical for understanding the impacts of climate change on forest and freshwater ecosystems.

Keywords: stream, lake, climate change, ecosystem services, LTER

Forest and freshwater ecosystems are intimately connected, and the ecological integrity of each depends on underlying processes and functions that the other provides. Forest ecosystems, dominated by trees and other woody vegetation, typically occur in the headwaters of many freshwater ecosystems (e.g., streams, rivers, ponds, lakes), and forest species composition, structure, and function strongly influence aquatic habitat and the quantity and quality of water resources (e.g., Ellison et al. 2012, Creed et al. 2019). Together, forests and associated freshwater ecosystems supply a myriad of goods and services that are essential for human well-being. Forests cover approximately 30% of the global land area (FAO and UNEP 2020) and provide important benefits including forest products, carbon sequestration, nutrient retention, and flood control. Freshwater ecosystems make up only a small fraction of the Earth's surface (less than 1%, Gleick 1996). However, they also provide essential services, such as water for drinking, irrigation, wastewater assimilation, power generation, fish and waterfowl habitat, and transportation (Postel and Carpenter 1997). Forest and freshwater ecosystems are inextricably linked and offer related benefits, including rich biodiversity, recreational opportunities, cultural significance, and aesthetics.

Climate change, including increasing climate variability, is altering the composition and functioning of forest and freshwater ecosystems, which affects their ability to provide ecosystem services (figure 1). Some of these changes are caused by subtle shifts in mean climate over time, which can elicit ecological responses that are often difficult to detect. Increased extreme weather events, including extreme heat and acute wet and dry conditions, arguably have greater impacts on ecosystems than gradual changes in mean climate (Smith 2011, Ummenhofer and Meehl 2017). Warming temperature, changes in precipitation, and increasing variability of each can manifest differently among regions. For example, the substantial warming in cold regions reduces the amount of frozen water by causing permafrost thaw, glacial melt, and decreased snowpack and lake ice cover, with profound effects, some of which feed back into the global climate system (Fountain et al. 2012). In tropical regions, small changes in otherwise steady temperature regimes also may have profound effects because tropical ecosystems have evolved under a narrower temperature range and may be more sensitive to warming (Wright et al. 2009).

Evaluating the impacts of climate change on forest and freshwater ecosystems is challenging because of co-occurring

BioScience 72: 851–870.
https://doi.org/10.1093/biosci/biab124 Advance Access publication 16 August 2022

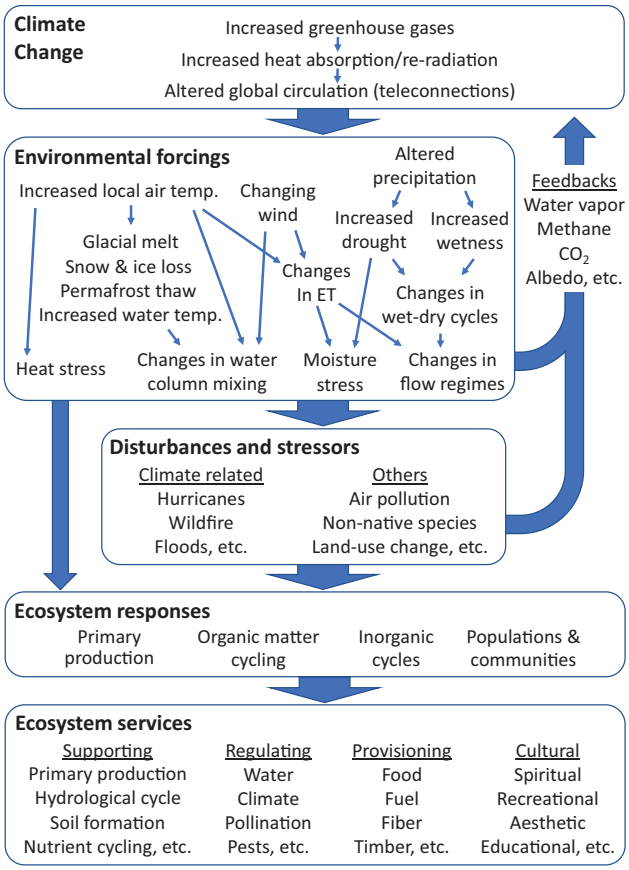


Figure 1. Conceptual diagram showing how climate change and associated ecological forcing elicit ecosystem responses and alter ecosystem services.

changes in other global change drivers that can influence responses. Factors such as atmospheric deposition of nitrogen and sulfur, increasing atmospheric carbon dioxide, and increasing tropospheric ozone can have antagonistic or synergistic effects that may counteract or amplify effects of climate change (Bytnerowicz et al. 2007, Baron et al. 2013). In addition, responses of forest and freshwater ecosystems to major disturbances, which may (e.g., extreme weather events, catastrophic wildfires) or may not be related to climate change (e.g., land-use change), introduce additional levels of complexity (figure 1; e.g., Ollinger et al. 2002).

Long-term ecological research has improved the scientific understanding of shifts in forest and freshwater ecosystem function caused by climate change and its variability. There is a pressing need to synthesize this information to inform resource management and help guide decision-making. In this article, we evaluate changes in climate and the effects of these changes at long-term ecological research (LTER) sites that have both forest and freshwater components. Our goals in this analysis are to characterize the range of climate changes observed across forest and freshwater sites of the US LTER Network and evaluate the responses of these ecosystems to changing climate. This article is part of a special issue that marks the 40th anniversary of the US National Science Foundation's Long Term Ecological Research (LTER) program. Companion articles in this special issue address the responses of coastal, dryland, and marine pelagic ecosystems to climate change, and an overview article compares and contrasts responses among these ecosystems.

Study sites

The US LTER Network consists of 28 sites located in many ecosystem types and biomes. In this analysis we focus on the nine LTER sites with linked forest and freshwater ecosystems (figure 2, table 1, supplemental material). Five sites (Andrews, Bonanza Creek, Coweeta, Hubbard Brook, and Luquillo) are US Forest Service Experimental Forests established between 1934 and 1963 and have long-term records from gauged, experimental watersheds to study how forest management and other ecological change impacts stream water quantity and quality. Although these watershed studies were not initially designed to study climate change, their long-term data sets have become invaluable for assessing climate change impacts. These five sites and the additional four sites were selected for this analysis because they have common research themes focusing on forest and freshwater ecosystems, even though site characteristics and research emphases vary by location. Average annual air temperature at these sites ranges from –3 degrees Celsius (°C) to 23°C and mean annual precipitation ranges from 270 to 3500 millimeters (table 1). The nine sites include a tropical rainforest (Luquillo, Puerto Rico [LUQ]), temperate rainforest (H. J. Andrews, Oregon [AND]), boreal forest (Niwot Ridge, Colorado [NWT], and Bonanza Creek, Alaska [BNZ]), and five temperate forest sites, including one in the north-central United States (North Temperate Lakes, Wisconsin (NTL) and four that are in relatively close proximity along a latitudinal gradient in the eastern United States (Hubbard Brook, New Hampshire [HBR]; Harvard Forest, Massachusetts [HFR]; Baltimore Ecosystem Study, Maryland [BES]; and Coweeta, North Carolina [CWT]).

These LTER sites have a history of climate change research using a combination of approaches including long-term monitoring, field and laboratory experiments, dendroclimatology, paleoecology, and modeling. The LTER Network is bottom-up in the sense that the research is investigator-driven and has a broad scope with questions that vary from site to site. Although this design makes cross-site analyses challenging, the focus on long-term place-based observational studies and experimental manipulations (see supplemental table S1) enables in-depth research that provides mechanistic understanding of ecosystem function and response to change.

Recent changes in air temperature and precipitation

To put ecosystem responses to climate change in context, we examined changes in climate at the nine forest and freshwater LTER sites on time scales relevant to the long life spans of trees, including the LTER period (1980–2019) relative

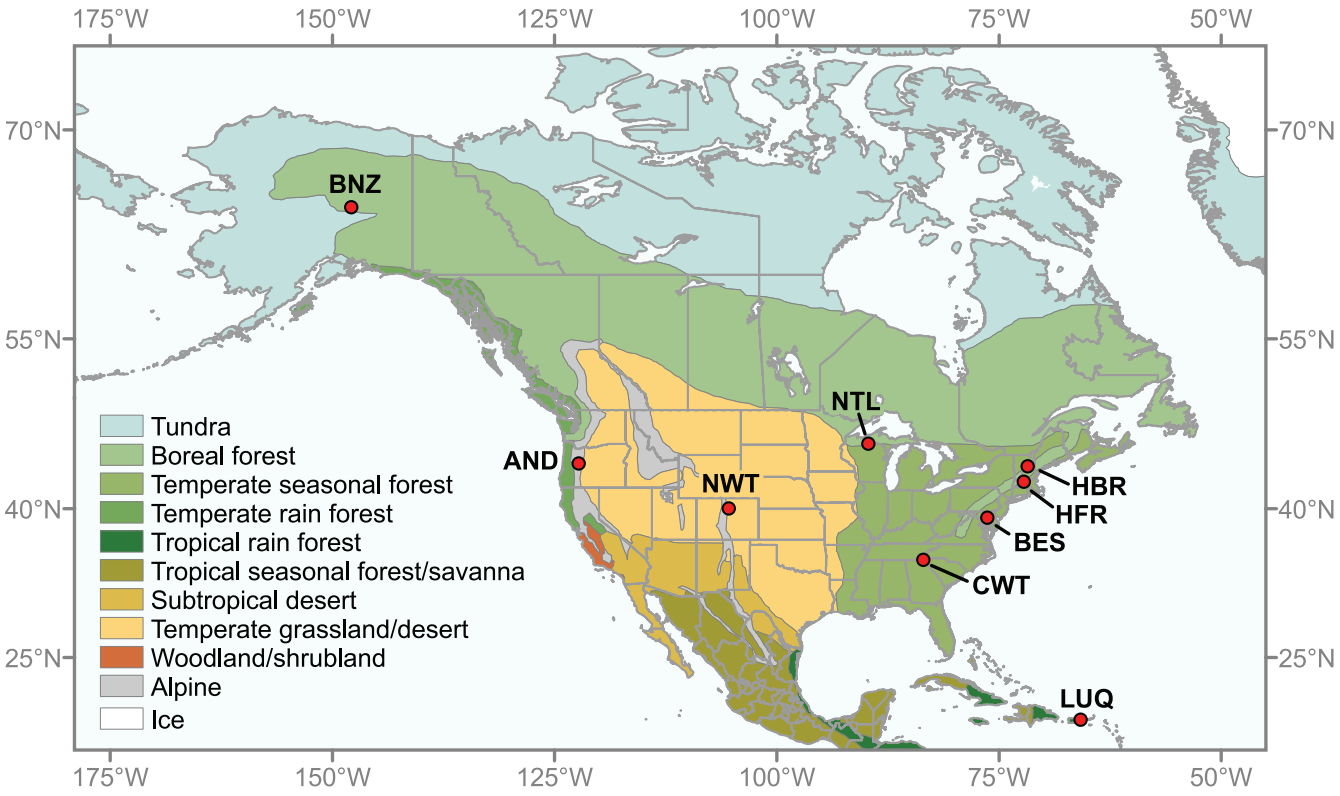


Figure 2. Study sites in the Long Term Ecological Research Network representing forest and freshwater ecosystems.

to the twentieth century (1900–1999) reference period, the current period (2010–2019) relative to the late twentieth century reference period (1970–1999), observed 70- and 50-year trends (1950–2019 and 1970–2019) and projected future trends (2020–2099), and recent climate (1990–2019) versus projected future climate (2070–2099). We used publicly available gridded data sets because of the need to make comparisons on the basis of consistent data sources among disparate sites, and to characterize changes that extend over longer periods than the LTER program (Jones and Driscoll 2022, this issue). Monthly temperature and precipitation data for each LTER site were extracted from 0.5-degree grid cells for the period from 1900 through 2019 from the University of East Anglia's Climatic Research Unit gridded data product (CRU TS4.04; Harris et al. 2020). Gridded climate data provide an indication of regional trends in climate at each LTER site and are well correlated to LTER measurements (supplemental figures S1a and S1b), despite some differences in mountainous areas. Gridded temperature and precipitation data, as well as other time series data in this manuscript, were analyzed for significant trends ($p < .05$) using the nonparametric Mann–Kendall test (Kendall 1938, Mann 1945). Slopes were calculated as the median slope of all possible pairs in the data set as described by Sen (1968).

Mean annual air temperature increased significantly at all sites from 1950 to 2019, with rates ranging from 0.09°C per decade at Niwot Ridge to 0.39°C per decade at Bonanza Creek (table 2). Precipitation also increased from 1950 to 2019 at sites in the eastern United States (Baltimore, Coweeta, Hubbard Brook, Harvard Forest), and lesser but statistically significant increases also occurred at Niwot Ridge in the West. Similar patterns were evident over a shorter period when streamflow data were available for all sites (1970–2019), but trends in precipitation for this shorter period, although they are generally consistent with trends for the longer period, were not significant (table 2). More rapid warming at poleward LTER sites and increased precipitation in the eastern United States are consistent with broadscale analyses (USGCRP 2017, Dai et al. 2019).

In the LTER period (1980–2019), the frequency of hot and cold months reflects climate change effects relative to the twentieth century (1900–1999) in absolute (figure 3a, 3b) and relative (figure 3c, 3d) terms. Hot months were defined in absolute terms as those with temperature more than 2°C above, and cold months were defined as those with temperature more than 2°C below the mean monthly temperature for the reference period (1900–1999; figure 3a, 3b). The 2°C value is commonly used as a policy target for maximum allowable warming (Randalls 2010), and is slightly less than twice the total current global average air temperature increase since preindustrial times (1.1°C from 1880 to 2020; NOAA 2021). Extreme hot (cold) months were defined in relative terms as those with temperature above the 90th percentile (below the 10th percentile) for the twentieth century

Table 1. Characteristics of forested Long Term Ecological Research sites.

Site	Latitude	Longitude	Elevation (in meters)	Mean annual temperature (in degrees Celsius)	Mean annual precipitation (in millimeters)	Cover type
Baltimore	39°06'N	76°18'W	2	13	1040	Mixed hardwood
Bonanza Creek	64°52'N	147°51'W	365	–3	270	Boreal forest
Coweeta	35°00'N	83°30'W	686	13	2100	Mixed hardwood
H. J. Andrews	44°13'N	122°15'W	1020	9	2250	Douglas fir or western hemlock
Harvard Forest	42°32'N	72°11'W	330	8	1090	Transition hardwood or white pine or hemlock
Hubbard Brook	43°56'N	71°45'W	590	6	1400	Northern hardwood or spruce fir
Luquillo	18°18'N	65°48'W	350	23	3500	Tropical hardwoods
Niwot Ridge	40°02'N	105°33'W	3020	2	680	Subalpine conifer
North Temperate Lakes	46°01'N	89°40'W	497	4	820	Red and white pine or northern hardwood

Table 2. Trends in mean annual temperature, precipitation, and the Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al. 2010) from 1950 to 2019 as determined with gridded climate data (CRU TS4.04; Harris et al. 2020).

	1950–2019			1970–2019			
Site	Air temperature (in degree Celsius [°C] per decade)	Precipitation (in millimeters [mm] per decade)	SPEI per decade	Air temperature (in °C per decade)	Precipitation (in mm per decade)	SPEI per decade	Streamflow (in mm per decade)
H. J. Andrews	**0.12**	–9	0	**0.18**	–20	–0.01	–46
Baltimore	**0.16**	**22**	**0.05**	**0.23**	21	0.04	6
Bonanza Creek	**0.39**	1	–0.01	**0.49**	2	–0.02	7
Coweeta	**0.15**	18	0.03	**0.28**	–2	0.01	–45
Hubbard Brook	**0.19**	**29**	**0.06**	**0.32**	34	0.07	34
Harvard Forest	**0.2**	**25**	**0.04**	**0.28**	25	0.05	22
Luquillo	**0.2**	20	0.02	**0.22**	90	0.09	84
North Temperate Lakes	**0.16**	6	0.03	**0.24**	13	0.06	6
Niwot Ridge	**0.09**	**9**	**0.04**	**0.24**	9	0.05	1

Note: Trends from 1970 to 2019 are also shown, which is the period when streamflow data are available. Values in bold font indicate significant trends (i.e., a significant increase (positive slope) or decrease (negative slope) in the time series as determined with a Mann–Kendal test (Kendall 1938, Mann 1945) at $p < .05$).

(figure 3c, 3d). Increases in frequency of hot months and losses of cold months in absolute terms were negatively related to mean annual temperature (figure 3a, 3b). In contrast, the frequency of extreme hot and cold months in relative terms was less related to mean annual temperature (figure 3c, 3d). Relative increases for the LTER period were greatest at Luquillo (tropical rainforest), exceeding the 90th percentile 6 months per year on average, compared with other sites that exceeded the 90th percentile about 2 months per year (figure 3c). Monthly temperature during the LTER period was never below the 10th percentile at Luquillo, with other sites being below the 10th percentile an average of 0.3–0.8 months per year (figure 3d). In summary, at most sites hot temperature thresholds were exceeded more frequently than cold temperature thresholds, both in absolute and relative terms. In addition, absolute temperature changes were greatest at colder sites and least at the tropical forest site, but relative changes were greatest at the tropical forest site.

Future changes in air temperature and precipitation

We tested whether projected climate change through the end of the twenty-first century will push LTER sites outside

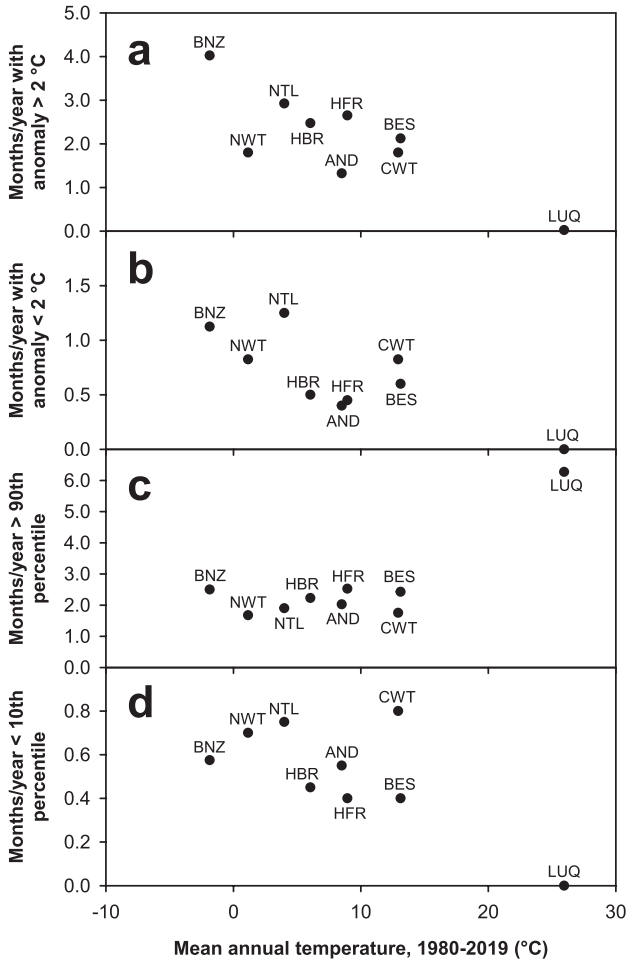


Figure 3. Number of months per year air temperature for the LTER period (1980–2019) was greater than 2°C above (a) and less than 2°C below the twentieth century mean (b), and greater than 90th percentile (c) and less than 10th percentile (d), as a function of recent (1980–2019) mean annual air temperature.

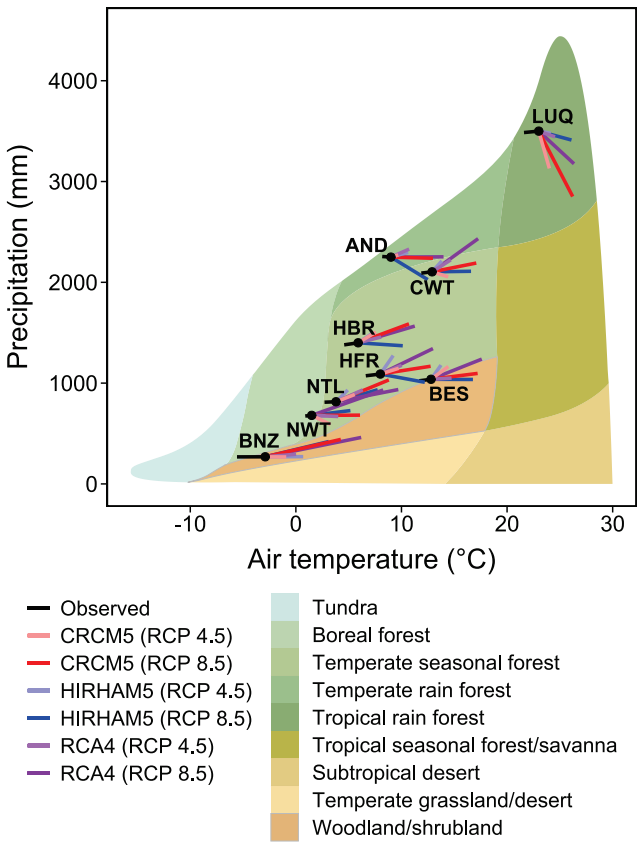


Figure 4. Forest and freshwater LTER sites plotted as a function of temperature and precipitation in relation to biome type (Whittaker 1975). The black lines indicate the slope of observed trends (1950–2019) and the colored lines indicate projected future trends (2020–2099) based on output from regional climate models.

the ranges of mean annual temperature and precipitation for forest biomes defined by Whittaker (1975), to evaluate the potential for future biome shifts at LTER sites. We plotted historical (1950–2019) and projected future (2020–2099) mean annual temperature and precipitation for each forest and freshwater LTER site on Whittaker's (1975) biome classification (figure 4). Historical data were obtained from the CRU TS4.04 source described previously (Harris et al. 2020), and projected future data were obtained from the North American Coordinated Regional Climate Downscaling Experiment database (2020–2099; Mearns et al. 2017). Future climate projections include output from three regional climate models (CRCM5-UQAM, HIRHAM5, RCA4) driven by three different global climate models (MPI-ESM-LR, EC-EARTH, CanESM2, respectively) and two representative concentration pathways (RCP 4.5 and 8.5). Bias-corrected data (Maraun 2016) were extracted from 50-kilometer grid cells corresponding to LTER site locations. Characteristics of the regional climate models are summarized by Mearns et al. (2017) and described in detail by Šeparović and colleagues (2013) for CRCM5-UQAM, Christensen and colleagues (2007) for HIRHAM5, and Samuelsson and colleagues (2011) for RCA4. Descriptions of the global climate models are provided by Flato and colleagues (2013) and representative concentrations pathways by Moss and colleagues (2010).

The current climate at each forest and freshwater LTER site generally reflects the current biome type defined by Whittaker (1975) on the basis of mean annual temperature and precipitation. Recent changes (1950–2019) are relatively minor compared to projected future changes (2020–2099; figure 4), indicating that although few forest biome shifts have been observed, they may occur in the future. Temperature and precipitation changes projected under future scenarios, shift some LTER sites (i.e., Baltimore, Bonanza Creek, Niwot Ridge, Andrews, Coweeta) into a climate space (i.e., as it was defined by Whittaker (1975) on the basis of mean annual temperature and precipitation) associated with a different biome, but other sites (i.e., Hubbard Brook, Harvard Forest,

Luquillo, North Temperate Lakes) remain within the climate space of their current biome (figure 4). Biomes can exist outside their typical climate space because of factors such as soil, legacies of disturbance, and seasonality of precipitation (Whittaker 1975). Therefore, ecosystem changes beyond temperature and precipitation will also likely influence the future biomes of forest and freshwater sites. In addition, biome shifts have occurred under observed changes in temperature and precipitation, because of climate-related stressors or disturbances that accelerate transitions. For example, at Bonanza Creek in interior Alaska, temperature and precipitation from 1950 to 2019 is characteristic of the boreal forest biome (figure 4); however, areas dominated by conifer forests in this region are increasingly shifting to broad-leaved forests, a change that has been attributed to the increased intensity of wildfires resulting from drier conditions (Juday et al. 2015, Mack et al. 2021). Biome shifts such as this have been documented around the world and will become more prevalent with more pronounced future changes in temperature and precipitation (Gonzalez et al. 2010), having important social–ecological repercussions (e.g., Chapin et al. 2010).

Changes in the water balance and hydrology

A critical uncertainty is how changes in climate will influence the hydrology of forest and freshwater ecosystems. Decreases in precipitation and increases in temperature that increase evapotranspiration would likely shift forests toward water-limited conditions (Jones et al. 2012). However, increases in precipitation, thawing of permafrost, glacial melt, or decreases in transpiration could offset water limitation. To represent climate changes affecting moisture, we evaluated trends in water limitation with Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al. 2010) data from the Global SPEI database (Beguería et al. 2010, SPEIbase 2021), which is derived from the historical climate data (CRU TS4.04, Harris et al. 2020). The SPEI uses monthly precipitation and potential evapotranspiration, in this case determined with the Penman–Monteith method (PET; Allen et al. 1998), to calculate a climatic water balance (P-PET). The values are standardized using a log-logistic distribution, making it possible to compare SPEI values across sites. Positive SPEI values indicate wetter conditions, whereas negative values indicate drier conditions. The SPEI index only includes precipitation and PET and does not capture hydrological changes associated with permafrost, snow, or glaciers.

In addition to changes in climate, forest ecosystems may be changing, both in response to climate change, as well as to past disturbances and subsequent succession. Therefore, changes in hydrology may reflect climate change directly, with no ecosystem response, or ecosystem change, with no effect of climate change, or some combination. To evaluate changes in the processing of water by forest and freshwater sites, we examined how changes in SPEI are related to changes in air temperature (figure 5a) and how changes in streamflow are related to changes in SPEI (figure 5b). Streamflow data were obtained from long-term monitoring programs established by the USDA Forest Service at three LTER sites (Coweeta, Hubbard Brook, and Andrews) and from US Geological Survey (USGS) gauging stations (USGS 2021) at the other six sites (Baltimore, Bonanza Creek, Harvard Forest, Luquillo, North Temperate Lakes, Niwot Ridge; see the supplemental material). For USGS data, a stream gauging station at or closest to each LTER site was selected from a subset of stations that make up the GAGES II network (Falcone 2011), which have watersheds that are minimally disturbed. For all sites, gauged reference watersheds with at least 50 years of continuous data (1970–2019) were used. The selected gauging stations are within 67 kilometers of LTER sites and drainage basins range from 0.1 to 963 square kilometers (supplemental table S2).

All the forest and freshwater LTER sites are becoming wetter as they become warmer, except for Andrews and Bonanza Creek, which are becoming drier (figure 5a, table 2); most LTER forest and freshwater sites are in the eastern United States and few are in the western United States, where climate is generally becoming drier (USGCRP 2017). Streamflow is increasing at Harvard Forest, Hubbard Brook, and especially Luquillo, consistent with increases in precipitation and SPEI. Streamflow at Andrews is decreasing, consistent with a slight decrease in SPEI and decreasing precipitation (figure 5b, table 2). Streamflow at Bonanza Creek is increasing slightly, despite declining SPEI, a response that may be due to thawing of permafrost, deepening of active layer depth, and resulting change in the routing of water through catchments (Jones and Rinehart 2010). Streamflow is decreasing slightly at Coweeta, despite increasing wetness, which is consistent with observed reductions in tree basal area and shifts in forest composition toward species with greater water demands resulting from disturbance and natural community dynamics (Caldwell et al. 2016). At other sites, streamflow increases are small (Baltimore, North Temperate Lakes) or negligible (Niwot Ridge), suggesting minimal response to climate change or counteracting effects.

We illustrate potential shifts in future seasonal dryness across forest and freshwater LTER sites by plotting the dryness index (ratio of potential evapotranspiration to precipitation) for the reference period (mean of 1990–2019) versus the latter part of the twenty-first century (mean of 2070–2099; figure 6). Similar to SPEI, the dryness index provides a quantitative measure of water surplus or deficit, where PET:P > 1 indicates water limitation and PET:P < 1 indicates energy limitation (Budyko 1974). Dryness index values for each site were calculated using past and projected future temperature and precipitation data described previously, and PET calculated with the Hamon (1963) method. During winter (December–February), all sites are energy limited and are projected to remain so under future climate change (figure 6a). During summer, dryness increases at all sites, except for Luquillo, which has a tropical climate that does not vary much throughout the year. Because most of

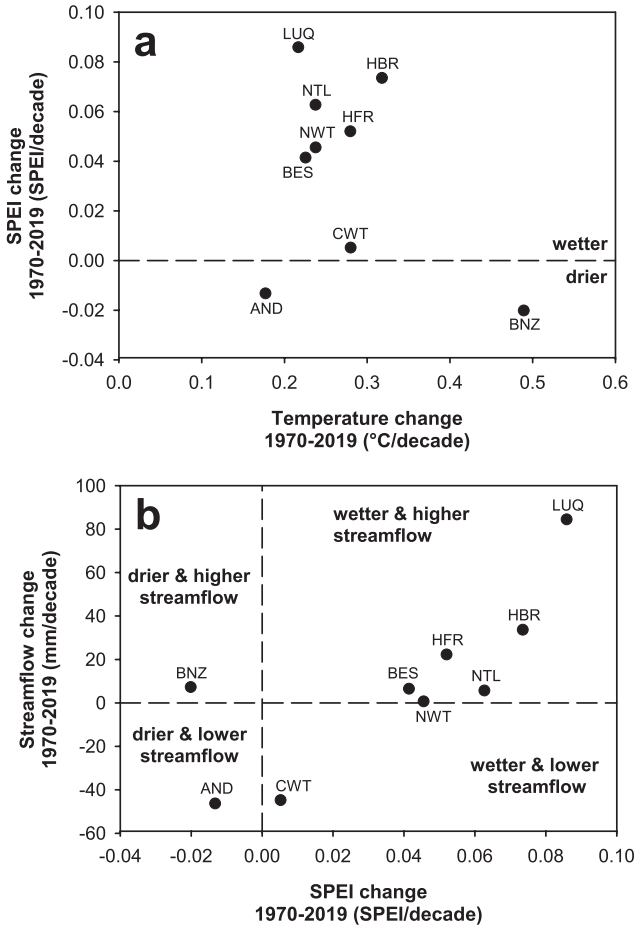


Figure 5. Trends in (a) the Standardized Precipitation Evapotranspiration (SPEI) index versus changes in air temperature and (b) streamflow versus changes in SPEI for 1970–2019. Trends in SPEI greater than zero indicate increasingly wet conditions and values less than zero indicate increasingly dry conditions.

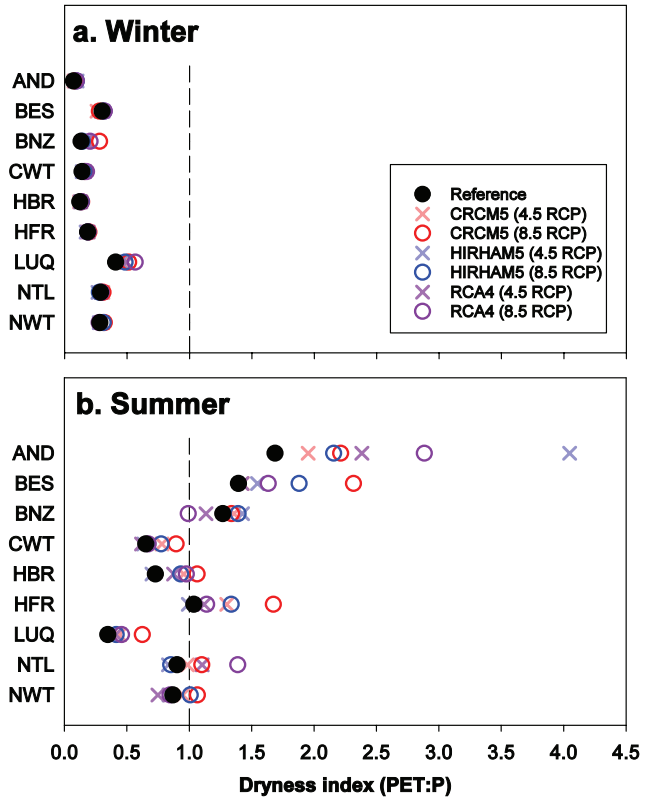


Figure 6. Dryness index calculated as the ratio of potential evapotranspiration to precipitation during (a) winter (December–February) and (b) summer (June–August) under the reference period (mean from 1990 to 2019) and future projected climate change (mean of 2070–2099) at forest and freshwater LTER sites. Values less than one (dashed line) indicate energy limitation, whereas values greater than one indicate water limitation.

the forest and freshwater LTER sites are in mesic climates they are not water limited in summer at present. However, summer dryness generally increases with climate change, and some sites show greater water limitation in the future, especially Andrews in the Northwest. These results suggest that summer dryness will become increasingly important, with many potential negative consequences, such as increased wildfire risk, decreased forest productivity, and lower streamflow.

Extreme events

Climate change is also altering extreme weather events that can have greater impacts than chronic changes in mean climate alone. Weather events have been studied at forest and freshwater LTER sites by examining the long-term ecosystem response to actual events and using experiments that mimic these disturbances (supplemental table S1; Thompson et al. 2013). The types of events that occur at each LTER site have shaped their respective research programs and lines of investigation. Climate warming is expected to increase the intensity of the hydrological cycle, with more frequent heavy precipitation events and longer, more intense droughts (Trenberth 2011). In addition, climate change is increasingly subjecting forest and freshwater ecosystems to disturbances, such as wildfire, hurricanes, and ice storms.

For the counties in which the nine forest and freshwater LTER sites are located, severe storms and floods are the most common extreme events that require federal financial support, on the basis of emergency declarations reported from 1965 to present by the Federal Emergency Management Agency (figure 7, supplemental material; FEMA 2020). Emergency declarations give an indication of the extent and severity of the disaster, number of people affected, and impacts on infrastructure. Hurricane emergencies occur along North Atlantic Ocean storm tracks, especially at Luquillo, fire emergencies occur at sites in the western United States and Alaska, and the greatest number of snow-related emergencies occur at Baltimore, not

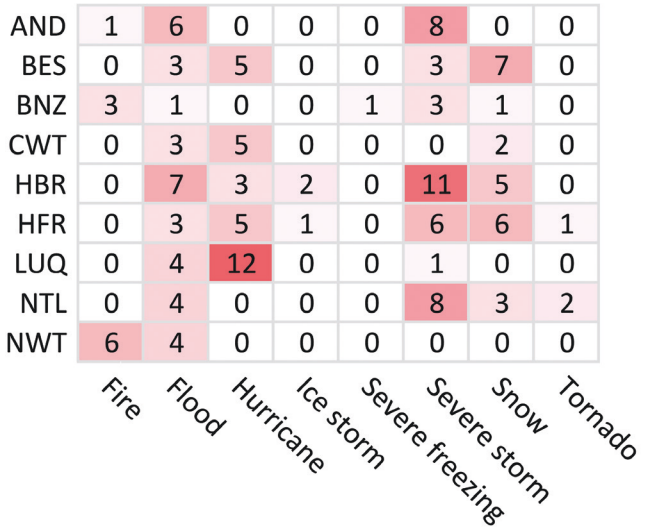


Figure 7. Heat map showing the number of weather-related disaster declarations for the county that each forest and freshwater LTER site is located in. Data are from the US Federal Emergency Management Agency Disaster Declarations Database (FEMA 2020) and cover the period from 1965 to 2020. Additional details about the methodology are provided in the supplemental material under the weather-related disasters section.

because it receives abundant snowfall relative to other sites but, rather, because of the disruption these events cause in this densely populated urban environment. Tornados (North Temperate Lakes, Harvard Forest), severe freezing (Bonanza Creek), and ice storms (Hubbard Brook, Harvard Forest) are relatively rare events at forest and freshwater LTER sites but can have long-lasting legacy effects (Dale et al. 2001).

Extreme events and related effects on vegetation influence forest water processing and transport to streams (Trenberth 2011). Therefore, changes in SPEI and streamflow extremes may reflect changes associated with the increased intensity of the hydrologic cycle. We assessed trends in extreme high and low precipitation at forest and freshwater LTER sites by comparing extreme SPEI values (greater than 90th and less than 10th percentiles) in the recent period (2010–2019) in comparison with the 1970–1999 period. The frequency of extreme wet months increased at most sites, decreased at Andrews and Harvard Forest, and showed little change at Baltimore (supplemental figure S2a). The decline in extreme wet months at Harvard Forest is difficult to explain, given the increases observed at nearby Hubbard Brook, indicating substantial variability within regions. The frequency of extreme dry months increased at Luquillo (tropical), Andrews and Niwot Ridge (western mountain), and Bonanza Creek (Alaska), and decreased at all the sites in the eastern United States (supplemental figure S2b). Therefore, extreme dry conditions are declining in the eastern United States, which is consistent with the regional increase in

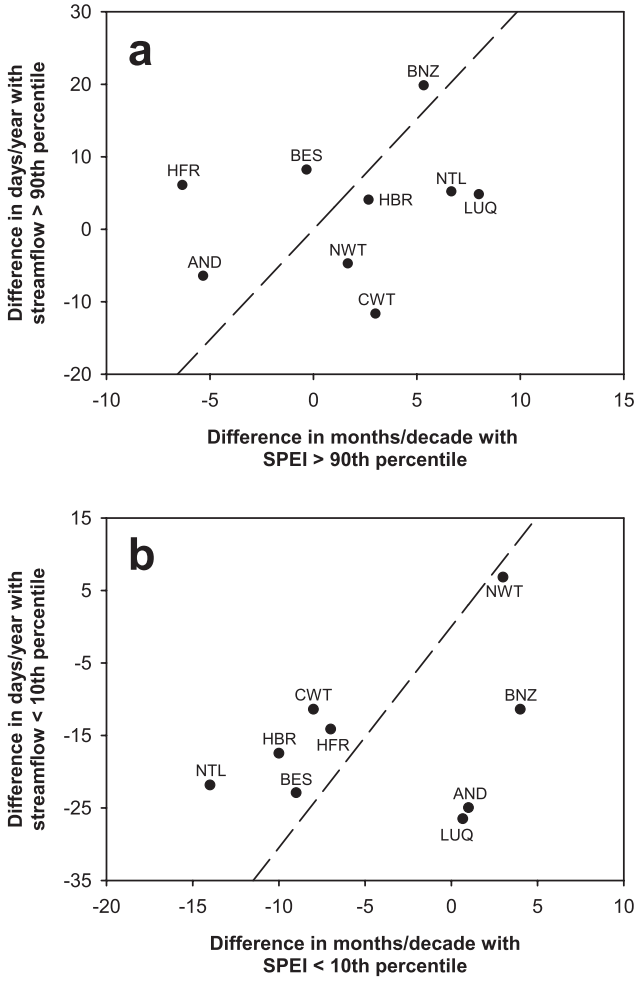


Figure 8. Change in the frequency of high or low flow days versus change in the frequency of extreme wet or dry months as was indicated by values greater than the 90th percentile (a) and less than the 10th percentile (b) for the recent period (2010–2019) compared to the reference period (1970–1999). The dashed line is the line of equal response. In panels (a) and (b), sites above or below the dashed line had a greater than or less than expected change in days with extreme high or low flows given the change in frequency of extreme wet or dry months.

precipitation (USGCRP 2017), whereas the other sites show a tendency toward more extreme dryness.

Extreme streamflow has responded to changing wet and dry conditions. In the past decade (2010–2019), the number of days with extreme high streamflow has increased relative to 1970–1999, especially at Bonanza Creek and to a lesser extent at Luquillo and most of the sites in the eastern United States (supplemental figure S3a). Reductions in high streamflow have occurred at Niwot Ridge, Andrews, and Coweeta. At most forest and freshwater LTER sites, extreme high streamflow has responded somewhat proportionally to changes in extreme wet conditions (figure 8a). Harvard Forest had more extreme high flows than expected on the

basis of the relationship with SPEI. In contrast, Coweeta, North Temperate Lakes, and Luquillo had fewer extreme high flows than expected on the basis of the increase in extreme wet months. This response suggests, in general, that some forest ecosystems are not effective in mitigating climate change-induced increases in extreme storm events, whereas others have some capacity to moderate flow increases associated with extreme wet conditions.

At most forest and freshwater sites, extreme low flows occur in the summer, when trees are transpiring, but in cold regions, extreme low flows occur in winter because of water storage in snow and ice (e.g., Bonanza Creek and Niwot Ridge). In 2010–2019, all sites except Niwot Ridge showed reductions in low flow days relative to 1970–1999 (supplemental figure S3b). Extreme low streamflow generally responded as expected to extreme dry months at most sites (figure 8b). At North Temperate Lakes and most eastern sites, extreme low flow days decreased in response to a reduction in extreme dry conditions. However, at Luquillo, Andrews, and Bonanza Creek extreme low flow days decreased, despite increases in extreme dry months. In other words, at sites at which precipitation increased, forests received additional growing season moisture, reducing the number of low flow days (table 2). At Bonanza Creek, permafrost thaw and reductions in snowpack depth and duration are shortening the winter period of extreme low flows (figure 8b), reducing low flow days. At Andrews and Luquillo, the reduction in extreme low flow days cannot be explained by changes in precipitation, temperature, or ice and may be due to changes in water use by forests undergoing succession after hurricane disturbance (Luquillo) or sixteenth and nineteenth century wildfire (Andrews). The nuanced relationships between forest disturbance and succession, climate, and streamflow highlight the need for continued study of the impacts of climate change on the hydrological cycle.

Environmental forcing due to changes in the phase and temperature of water

Increased energy inputs from a warming climate may produce changes in the phase of water (loss of snow and ice) in forest and freshwater ecosystems. Chronic loss of snow and ice reduces albedo, increases energy absorbed by forests and lakes, and further accelerates warming (Austin and Colman 2007, Euskirchen et al. 2016). Loss of snow and ice in forest watersheds increases winter streamflow and advances the timing and reduces the magnitude of spring snowmelt discharge (Dudley et al. 2017). Shallower snowpack also increases the potential for soil freezing events, which damage fine roots (Tierney et al. 2001) and may diminish plant nutrient uptake (Campbell et al. 2014). In addition, earlier snowmelt and a longer growing season can increase transpiration and summer soil moisture stress in forests, even in regions in which precipitation is increasing (Pourmokhtarian et al. 2017).

Increased energy inputs to freshwater ecosystems have reduced ice cover (Magnuson et al. 2000), as was demonstrated by long-term (38–167 year) records from LTER sites, including the Tanana River in Alaska (Bonanza Creek); Mirror Lake, New Hampshire (Hubbard Brook); Trout Lake and Lake Mendota, Wisconsin (North Temperate Lakes); and Green Lake 4, Colorado (Niwot Ridge; figure 9). However, lake ice in and out dates are difficult to predict. For example, a recent analysis of Northern Hemisphere lakes showed that climate trends, local weather, and large-scale climate indices account for only 40%–60% of the variability in the timing of lake ice breakup (Magnuson 2021).

Consistent with declines in ice cover, lake surface water temperature has increased but is also difficult to predict because of many factors that contribute to the variability such as radiation, cloud cover, and light attenuation in the water column (O'Reilly et al. 2015). At North Temperate Lakes, water temperature trends vary among lakes, by depth, and by time of year, with the most rapid increases in the fall (Winslow et al. 2017, Lathrop et al. 2019). Fall warming can increase the duration of summer stratification (Woolway et al. 2020) and prolong the period of low oxygen (Ladwig et al. 2021). In streams, water temperature has increased with air temperature (Kaushal et al. 2010), although local, site-related factors, such as groundwater contributions and riparian forest cover can affect the relationship (Arismendi et al. 2012, Arismendi et al. 2014). For example, at Andrews, gradual reductions in snowpack, increases in summer air temperature, and declining summer precipitation are associated with reduced streamflow and stream network contraction (Ward et al. 2020), conditions that are linked to warmer stream temperature (Arismendi et al. 2013). However, stream water contributions from groundwater sources during summer (Segura et al. 2019) and increased shade from regenerating riparian forests (Warren et al. 2016) can counteract these effects. In summary, increases in energy inputs to forest and freshwater ecosystems are decreasing water storage in snow, ice and groundwater and increasing the length of the growing season, which is influencing the volume and timing of streamflow, but effects on surface water temperature vary depending on local factors.

Ecosystem responses to climate change

The LTER program addresses five core research themes that all sites focus on. We frame our discussion of forest and freshwater ecosystem responses to climate change around four of these themes (primary production, accumulation and loss of organic matter, movement of inorganic matter, and populations and communities), with the fifth theme (disturbance) underlying all of the other themes.

Primary production. The complexity of changes in temperature and moisture on primary production are reflected in long-term trends at forest and freshwater LTER sites (e.g., see box 1) and are central to understanding the capacity for carbon sequestration. Increased air temperature and a longer growing season may increase forest primary productivity in energy-limited systems, and decrease it in water-limited systems (Liu

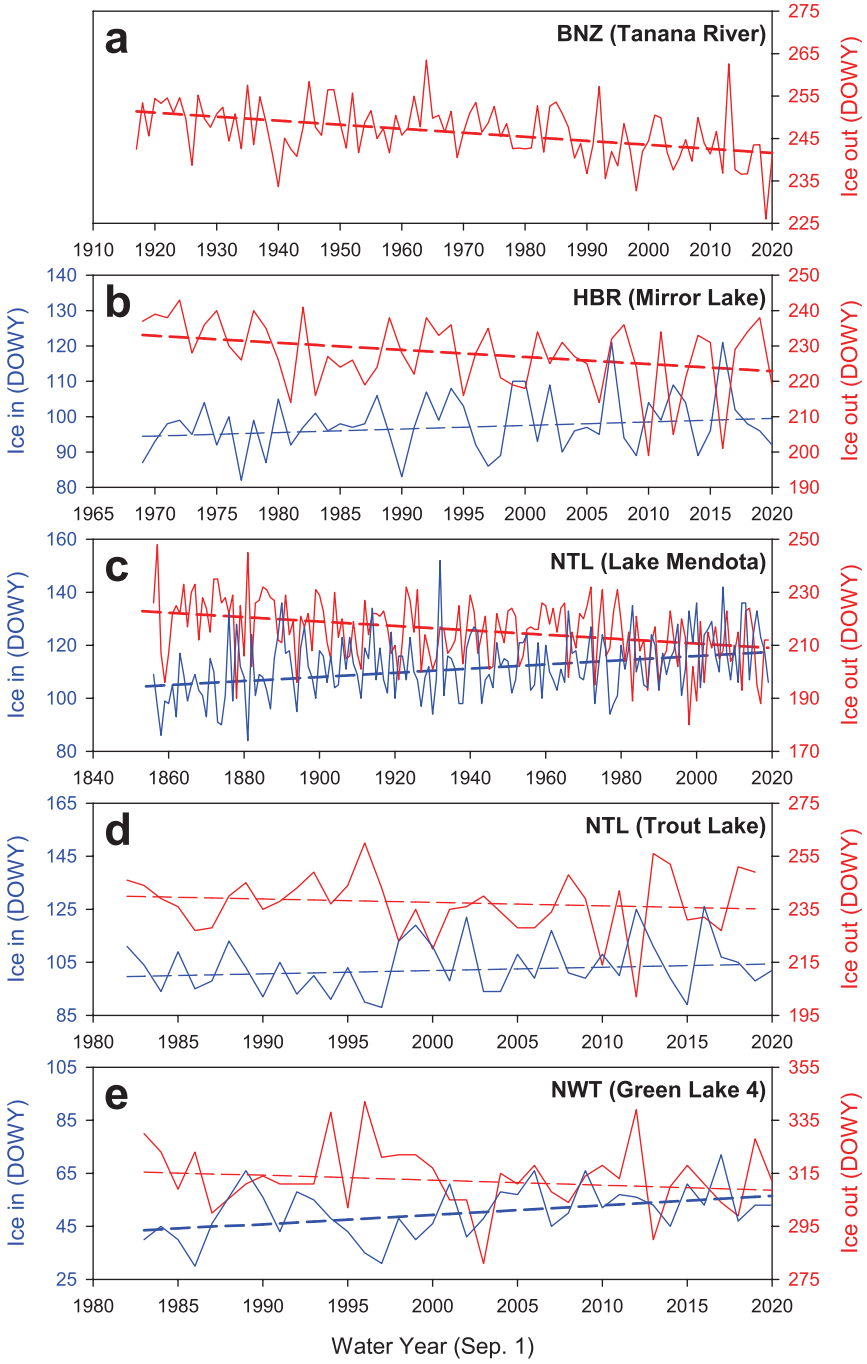


Figure 9. Long-term changes in lake and river ice in (blue lines) and ice out (red lines) dates as determined with site-specific criteria (see supplemental material). Dashed lines are the slope (Sen 1968) and bold lines indicate significant trends as determined with the Mann–Kendall test (Kendall 1938, Mann 1945) at $p < .05$. Sources: (a) Meier and Dewes (2020), (b) Likens and colleagues (2020), (c) Magnuson and colleagues (2020a), (d) Magnuson and colleagues (2020b), (e) Caine and colleagues (2020).

et al. 2019), but simultaneous changes in respiration may offset impacts on net primary production (the difference between carbon gained by photosynthesis and carbon released through respiration; Duveneck and Thompson 2017, Oishi et al. 2018). Even within sites, landscape variability and related effects of changes in temperature and moisture may influence the balance between carbon gains and losses. For example, in the mountainous terrain at Coweeta, cold air drainage and pooling in valleys reduces aboveground respiration during the growing season, resulting in a greater than 15% increase in annual net carbon uptake (Novick et al. 2016). Consequently, net ecosystem production in these lower elevation areas may be partially buffered from regional-scale climate change (e.g., Daly et al. 2010).

Climate-related disturbances can further confound effects of changes in air temperature and moisture on primary production. At Harvard Forest, a temperate forest undergoing regrowth following land abandonment, about one-third of the 26% increase in net primary production over a 20-year period was attributed to increases in temperature and growing season length (Finzi et al. 2020). However, these gains were offset by carbon losses from mortality of eastern hemlock (*Tsuga canadensis*) caused by the hemlock wooly adelgid (*Adelges tsugae*), an invasive insect whose spread is facilitated by warmer winters (Orwig et al. 2002). At other LTER sites, carbon losses from periodic climate-related disturbances such as hurricanes (e.g., at Luquillo; box 2; Hall et al. 2020), ice storms (e.g., at Hubbard Brook, Battles et al. 2014), fire (e.g., at Bonanza Creek, Mack et al. 2008), and drought (e.g., at Niwot Ridge, Smith et al. 2015) have been shown to limit or exceed gains as ecosystems recover.

Forest structure and developmental stage may influence the response and long-term trajectory of net primary production to climate change. For example, lower-stature, young stands are less susceptible to ice storm damage than mature stands (Rhoads et al. 2002), although tree size is not always a strong predictor of damage from hurricanes (Zimmerman et al. 1994). At Andrews, climate change has a greater influence on NPP in young forests than mature and old-growth forests, which are affected more by factors such as competition, small-scale disturbance, and microclimate (Woolley et al. 2015). In addition to impacts associated with stand age and structure, climate change also affects forest regeneration by

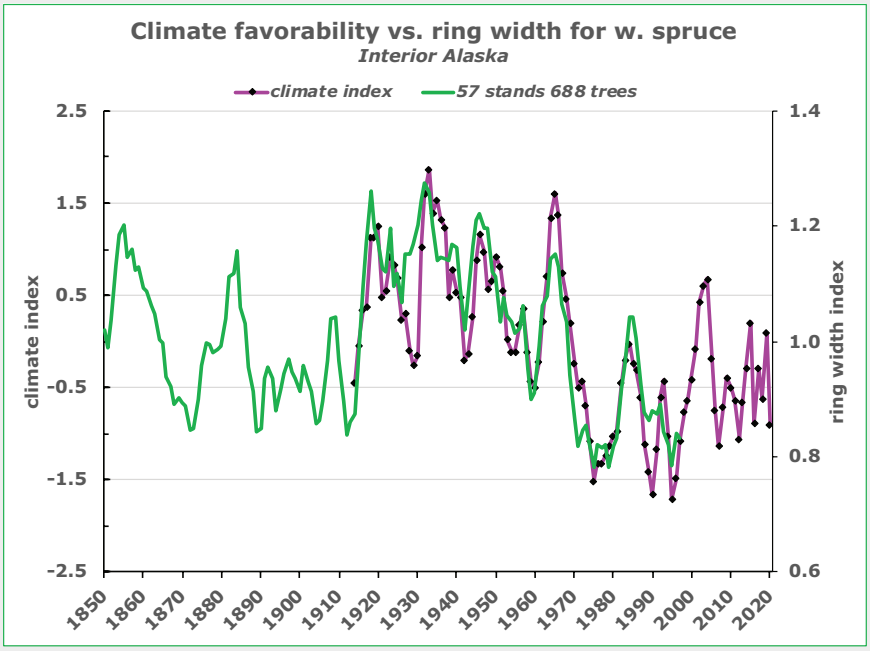
Box 1. Climate change and boreal forest growth at Bonanza Creek.

Climate change is amplified toward the Earth's poles (USGCRP 2017, Dai et al. 2019); therefore, boreal forests may act as sentinels of global warming. The far north has a long history of climate change research based on tree ring studies, and analyses of white spruce (*Picea glauca*) tree ring records at latitudinal and elevational treelines in Alaska made important early contributions to understanding relationships between past climate and tree growth (e.g., Giddings 1941). More recently, research at Bonanza Creek has provided important new insights on environmental controls of spruce growth that have been subsequently verified across the broader Alaskan boreal forest region (Barber et al. 2000, McGuire et al. 2010). A particularly surprising finding was that spruce growth throughout much of the dry interior region of Alaska was reduced when temperature was warmer because of moisture limitation (Juday et al. 2015). In contrast, spruce growth responded positively to summer warming at high elevations and in maritime western Alaska, where it is cooler and moister (Wilmking and Juday 2005, Juday et al. 2015). In these areas, growing season temperature is the dominant control over growth, and precipitation plays a supplemental positive role.

The predictive power of summer temperature and precipitation can be combined mathematically to produce an overall climate favorability index (CFI) that is useful for evaluating growth response to climate change (Juday and Alix 2012). Comparing the CFI with an index of tree ring growth for large white spruce at Bonanza Creek and numerous similar stands of interior Alaska (dry and warm summer region) reveals a remarkably strong and consistent relationship (see graph). These results indicate that tree ring records can be used reliably to reconstruct past climates before instrument records (about 1900) in this region (Juday et al. 2003).

In interior Alaska, quasidecadal cycles of climate favorability and tree growth have occurred since 1850, with a peak in the first half of the twentieth century and lowest values from 1975 to 2000. The unprecedented late twentieth century reduction in spruce growth is consistent with strong warming at Bonanza Creek (table 2) and a drying trend as was indicated by the Standardized Precipitation Evapotranspiration (SPEI) index (figure 5). A strong and prolonged La Niña from 1999 to 2003 provided substantial, but only brief, relief from hot dry conditions. However, near-record summer precipitation in interior Alaska since 2014, coincident with the exceptional warmth of the North Pacific Ocean and decline of Arctic sea ice cover, has produced an unprecedented climate regime of warm and moist conditions (Barber et al. 2004), which is associated with a modest recovery of spruce growth. It is not yet clear whether increased summer precipitation will continue to enhance boreal tree growth as anticipated additional warming occurs (figure 6b), so the question of increased versus decreased growth remains in the balance.

Continued monitoring of the profound and pervasive ecological responses to climate change in Alaska's boreal forest is critical for informing environmental policies and guiding land management decisions, such as those related to forest harvesting, wildfire, assisted migration, and carbon balance. Because of the rapid changes in climate in the far north, and importance of feedback into the global climate system, these forests will likely continue to serve as important early indicators of change.



influencing seed production and seedling establishment. At Andrews, a continuous 62-year record shows that the conifer cone crop, an indicator of seed supply, is cyclical and responsive to climate and other environmental cues (Franklin 1968, Pham et al. 2013). At Bonanza Creek, episodic seed production of white spruce (*Picea glauca*) also depends on a combination of specific weather conditions, including growth-limiting water stress 1–3 years prior to

Box 2. Ecosystem response in hurricane simulation experiments.

The frequency of intense hurricanes and geographic range of their impacts is increasing. In anticipation of this, two LTER forest sites, Harvard Forest and Luquillo, undertook experimental approaches to better understand the effect of hurricane disturbance on vegetation and biogeochemical dynamics of the forested ecosystems represented there (Cooper-Ellis et al. 1999, Foster et al. 2004, Shiels et al. 2015, Shiels et al. 2010). Interestingly, the two sites, one temperate and one tropical, used alternative methods to mimic hurricane damage but arrived at similar conclusions regarding the ecosystem responses. Post-disturbance, the resilience of trees, understory vegetation, and microbial processes exerted biotic control of ecosystem dynamics, particularly nutrient cycling.

At Harvard Forest, the Hurricane Experiment began in October 1990 in a 75-year-old oak–maple (*Quercus rubra–Acer rubrum*) stand, where selected canopy trees were pulled over with a winch and cable, using records from the 1938 hurricane to determine the number of trees felled and their direction of fall. The resulting damage to 65% of trees closely approximated effects of the 1938 storm, with uprooted trees providing great heterogeneity in soil conditions (i.e., pit and mound microtopography; Foster et al. 2004). At Luquillo, observations from Hurricane Hugo (1989) showed that removal of tree limbs by hurricane winds was the predominant immediate effect (Zimmerman et al. 1994). On the basis of this observation, hurricane damage was simulated by trimming tree canopies rather than downing whole trees. The Canopy Trimming Experiment (CTE) began in 2002, with treatments applied by a crew of arborists in late 2004 to early 2005. The CTE was a 2 × 2 factorial experiment, increasing canopy opening in two treatment plots and then moving debris from one trimmed plot to a third untrimmed plot (with a fourth serving as control). In this way, two main impacts of hurricane damage, canopy opening versus debris deposition, could be determined. The experiment was replicated in three blocks of forest dominated by *Dacryodes excelsa*. Canopy opening and amounts of debris were similar to that in Hurricane Hugo (1989).

The two experiments differed in the type of tree damage, which caused differences in soil disturbance and its heterogeneity as well as inputs of coarse (less than 10 centimeters in diameter) woody debris. The primary effects of hurricane disturbance in both studies were increased light levels and increased establishment of pioneer species, predominantly birch (*Betula* spp.) at Harvard Forest (Cooper-Ellis et al. 1999) and pumpwood (*Cecropia schreberiana*) and *Psychotria berteroana* at Luquillo (Shiels et al. 2010). No additional impacts on vegetation beyond the reduction in basal area associated with the physical application of the manipulation was observed at Harvard Forest (Cooper-Ellis et al. 1999), whereas at Luquillo, Shiels and colleagues (2010) noted no impacts of hurricane treatments on tree mortality; debris addition in the absence of canopy opening stimulated increased growth of tree basal area.

At Harvard Forest, there was remarkably little effect on ecosystem level variables, despite the increase in canopy openness and soil heterogeneity (Cooper-Ellis et al. 1999). At Luquillo, canopy opening, and not debris deposition, accounted for most of the changes in biotic processes (Shiels et al. 2015). Canopy opening at Luquillo decreased litterfall (as it did at Harvard Forest) and litter moisture, thereby inhibiting lignin-degrading fungi, which slowed rates of decomposition. Some changes in nitrogen processing were noted at both sites. At Harvard Forest, the effects were local in scale and minor in comparison to the overall nitrogen budget (Foster et al. 2004). Elevated soil solution nitrate was a dominant response at Luquillo, particularly where canopy-opening and debris treatments occurred simultaneously as in a hurricane, appearing to explain the increased levels of nitrate noted in streams posthurricane (Shiels et al. 2015). These effects were transitory in nature, only lasting a year or so postdisturbance.

Hurricane manipulation experiments

Luquillo (2005)
Photograph: Aaron B. Shiels

Harvard Forest (1990)
Photograph: John F. O'Keefe, Harvard Forest

masting events, but seed viability responds positively to wet and warm conditions during the seedfall year and is greatly reduced by drought stress (Juday et al. 2003, Roland et al. 2014). Moisture can also strongly control seedling recruitment—for example, in the subalpine forest at Niwot Ridge, where the establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) seedlings depends on soil moisture from above average snowpack and cool, wet summers (Andrus et al. 2018). Therefore, climatic conditions for forest regeneration are changing, which can have lagged, long-term effects on forest productivity.

In freshwater ecosystems, warmer water temperature and a longer ice-free season increase primary production. For example, warmer temperature increased primary production in a high-elevation lake at Niwot Ridge, because it reduced snowmelt and summer stream flow, increasing hydraulic residence times. In addition, enhanced permafrost thaw and glacial melting, increases lake solute inputs that fuel production (Preston et al. 2016). The combination of warmer water temperature and high nutrient loading can promote growth of cyanobacteria and harmful algal blooms that negatively affect aquatic habitat and human health (Paerl and Huisman 2008). Although climate change generally increases production in freshwater ecosystems, carbon gains can be offset by respiration losses, much like in forest ecosystems. For example, in a study of stream metabolism across six biomes from the tropics to the Arctic, Song and colleagues (2018) found that a 1°C increase in stream temperature caused a nearly 25% overall decline in net ecosystem productivity because of a change in the ratio of gross primary production to ecosystem respiration. These results indicate that warming-induced shifts in the metabolic balance may cause an overall increase in carbon dioxide emissions from streams.

Accumulation and loss of organic matter. Climate change affects organic matter cycling in forest and freshwater ecosystems largely by altering litter supply, decomposition, and microbial activity. Climate change is increasing extreme weather events and other disturbances, which can cause a pulse of litter inputs to the forest floor. For example, an ice storm in 1998 at Hubbard Brook deposited the equivalent of 10 years of average coarse litterfall (Fahey et al. 2005), and Hurricane Hugo at Luquillo deposited 1.2–1.9 times the average annual fine litterfall (Lodge et al. 1991). Wildfire can also increase litter inputs for several years, as foliage and coarse wood fall due to tree injury and mortality (Grigal and McColl 1975); however, wildfire differs from other climate-related disturbances in that it consumes forest floor litter, thereby reducing the soil carbon stock (Mack et al. 2021). The initial pulse of litter caused by disturbances is followed by a more prolonged, but highly variable period of lower litterfall as the forest canopy recovers (e.g., Vogt et al. 1996). If changes in litterfall are sustained they can affect decomposition and carbon loss, as was demonstrated by results from a network of long-term experiments involving litter and wood addition to soil that incudes decades-long investigations at Andrews and Harvard Forest (Lajtha et al. 2018).

Warming accelerates decomposition of soil organic matter, which could release more carbon dioxide to the atmosphere, creating a positive feedback loop (figure 1; Knorr et al. 2005). A long-term experiment at Harvard Forest that began in 1991, showed that soil warming initially stimulated soil respiration, although this effect diminished over time because of factors such as changing substrate quality, nutrient availability, moisture, and microbial biomass, carbon use efficiency and community structure (Frey et al. 2013, Melillo et al. 2017). Long-term studies such as this provide insight that can only be discerned by evaluating responses over many years. They are also critical for understanding the complex interactions and cascading effects of climate change. For example, in interior Alaska, the shift from boreal forest to broad-leaved deciduous forest due to increased wildfire size and intensity (Mack et al. 2021) has reduced soil moisture, carbon, and nitrogen, because of the higher evapotranspiration and more readily decomposable litter of deciduous species (Alexander and Mack 2016). Wildfire also consumes the insulating soil organic layer, leading to thawing of permafrost, decomposition of previously frozen organic matter, and further loss of soil carbon that produces a positive feedback loop to climate warming (Schuur et al. 2009). However, replacement of slow-growing conifer species with fast-growing deciduous species can result in a net increase in soil carbon storage over time (Mack et al. 2021). Understanding these complex interactions controlling carbon losses and feedback loops is critical for predicting future climate change.

In freshwater ecosystems, climate also strongly regulates organic matter supply and loss. The increases in coarse and fine litter inputs due to climate-related disturbances contribute to stream debris dam formation that retains particulate organic carbon (POC; e.g., Bilby 1981, Kraft et al. 2002), although this material may be released during floods (Swanson et al. 1998, Dhillon and Inamdar 2014). Stream litter breakdown increases with warming; however, the proportion of carbon loss from respiration and POC should not change with temperature because the temperature sensitivity of microbes and detritivores is similar (Follstad Shah et al. 2017). In addition to climate change, nutrient pollution can further increase breakdown and loss of terrestrially derived carbon in streams, as was demonstrated by a stream nitrogen and phosphorus enrichment experiment at Coweeta, in which 83% of the variation in carbon loss was explained by discharge, nitrogen, phosphorus, and temperature (Rosemond et al. 2015). Therefore, the standing stock, processing, and loss of carbon in streams is controlled by climate as well as nutrient availability.

In addition to stream carbon losses via respiration and POC, a small but important fraction is also exported as dissolved organic matter (DOM; Schlesinger and Bernhardt 2020). Changes in DOM have implications for the structure and function of freshwater ecosystems because it is a

primary substrate for the aquatic food web and protects organisms from damaging ultraviolet light (Williamson et al. 1996). However, elevated DOM can have negative effects, such as promoting the formation of oxidizing radicals (Wasswa et al. 2020), and enhancing the transport and altering the bioavailability of toxic metals such as mercury and aluminum (Driscoll and Postek 1996, Dittman et al. 2010). Long-term studies in temperate regions of North America and Europe have reported increases in the mobilization of DOM to surface waters, attributed both to both climate change and recovery from acid deposition (Monteith et al. 2007, Clark et al. 2010). Although positive relationships between temperature and DOM have been reported, the results are inconsistent, and warming is thought to account for a small portion of DOM increases (10%–20%). However, DOM export tends to increase with discharge, and could therefore increase in regions in which climate change is causing more frequent and intense storms (Raymond et al. 2016). In summary, the effects of climate change on organic matter in freshwater ecosystems varies, depending on factors such as litter inputs, decomposition, and hydrologic change.

Movement of inorganic matter. Mineralization of organic matter controls the supply of inorganic matter through processes governed by biological and climatic drivers. Disturbances that damage vegetation aboveground—for example, ice storms (Houlton et al. 2003) and hurricanes (McDowell and Liptzin 2014), and belowground—for example soil freezing (Campbell et al. 2014) can cause large losses of nutrients from forest ecosystems because of a combination of release from litter inputs and reduced plant uptake. The long-term soil warming experiment at Harvard Forest, as well as a study initiated in 2012 at Hubbard Brook, showed that in temperate forests, increased soil temperature increases nitrogen mineralization and nitrification during the growing season (Butler et al. 2012, Harrison et al. 2020). However, these effects may be offset by a shallower snowpack and colder soils during winter (Durán et al. 2016) or changes in soil moisture (Groffman et al. 2009). Inorganic cycles in tropical rainforests also are sensitive to climate change. At Luquillo, increased drought caused oxidation of soil iron, a reduction in phosphorus availability, and declining tree growth (O'Connell et al. 2018). Modeling indicates that the tropical forest carbon balance at Luquillo may shift from a net sink to a net source by the mid 2030s as a result (Feng et al. 2018). Therefore, the effects of climate change on nutrient availability in forest soils can have important implications for the carbon balance.

The impacts of climate change on inorganic matter cycling can also substantially affect freshwater ecosystems because of changes within surface waters and adjacent forest watersheds. Increased extreme streamflow, which is occurring at many sites (figure 8a), may increase the mobility and delivery of inorganic matter to streams. For example, at North Temperate Lakes, data collected over more than two decades show that increased extreme precipitation events have increased inputs of stream water phosphorus to Lake Mendota, making it more susceptible to algal blooms (Carpenter et al. 2018). Decreases in lake ice cover duration have reduced nitrate accumulation under ice, altering lake chemical and biological properties (Powers et al. 2017). In Pond Branch, a forested watershed at the Baltimore LTER site, variations in stream nitrogen concentrations are sensitive to drought and interactions between groundwater and the riparian forest (Duncan et al. 2015). At Hubbard Brook, there has been a long-term tightening of the nitrogen cycle with decreases in soil nitrogen mineralization, nitrification, soil nitrous oxide production, and stream nitrate losses (Groffman et al. 2018). This pattern has been attributed to enhanced plant and microbial demand for nitrogen because of factors such as a lengthening of the growing season, atmospheric carbon dioxide fertilization, decreases in atmospheric nitrogen deposition, increases in freeze–thaw cycles of soils, and recovery from elevated acid deposition. These examples illustrate how the cycling of inorganic matter is coupled with organic matter cycling, and highlight the importance of hydrologic change as well as global change drivers in regulating nutrient export.

Populations and communities. Climate is a key driver that shapes populations and communities in forest and freshwater ecosystems, and climate change may alter species' abundance and behavior, with impacts on community structure, composition, and function. In forests, climate change is shifting the biogeographic ranges of species; however, there is much uncertainty about the extent to which species can keep pace with climate change and how other interacting factors may influence migration. For example, at Niwot Ridge, increased air temperature, often associated with expansion of trees into the alpine zone, increases soil moisture limitation to limit future tree seedling recruitment (Suding et al. 2015, Conlisk et al. 2017). In the Pacific Northwest, drought extremes, rather than changes in mean climate, increased individual- and population-scale mortality of an understory tree, Pacific yew (*Taxus brevifolia*) across a wide geographic climate gradient (Germain and Lutz 2020). Climate extremes may therefore be more important than changes in average climate when predicting species range shifts.

Long-term data from forest and freshwater LTER sites also demonstrate how climate change is altering phenology and phenological synchrony in forest ecosystems. In a study of LTER sites representing diverse terrestrial ecosystems, warmer winters caused earlier bud break and lower consumer abundances in temperate forests, indicating that climate change may cause trophic mismatches between producers and consumers (Ladwig et al. 2016). On the other hand, some taxa respond synchronously to shifting climate. At Hubbard Brook, long-term (25-year) black-throated blue warbler (*Setophaga caerulescens*) data show that nesting activity is synchronized with leaf phenology to maximize annual reproductive success (Lany et al. 2016). In mountain forests at the Andrews, phenological events typically are delayed at high elevation, but in warm, dry years that

are representative of future climate change, phenology and microclimate are less variable and more synchronized from low to high elevation (Ward et al. 2018). These examples show that climate change is altering phenology in forest ecosystems, but shifts may be synchronous or asynchronous depending on the species and their environment.

Disturbances due to climate change are also affecting plant and animal populations and communities in forest ecosystems. For example, in the western United States, climate change has both increased wildfire and contributed to outbreaks of forest pests, such as the mountain pine beetle (*Dendroctonus ponderosae* Hopkins; Mietkiewicz and Kulakowski 2016), with some reciprocal interactions between wildfire and pine beetle disturbances (Creeden et al. 2014, Jenkins et al. 2014). The timescales at which populations and communities recover from climate-related disturbances may vary. After damage from Hurricane Hugo in the tropical rain forest at Luquillo, understory vegetation regrew within a few months, causing coqui frogs (*Eleutherodactylus coqui*, Woolbright 1996) and shrimp (*Atya lanipes*; Covich et al. 1991) to increase in abundance, whereas snail populations declined sharply after the storm, and then increased as their preferred plant species and habitat recovered (Secrest et al. 1996). Therefore, these plant–animal interactions are codependent and may produce delayed responses as ecosystems recover from disturbance.

In freshwater ecosystems, climate change may alter species assemblages, trophic structure, and food webs. At North Temperate Lakes, warmer lake temperature and lower dissolved oxygen decreased survival and reproduction of cisco (*Coregonus artedi*; Magee et al. 2019). The disappearance of cisco from some lakes negatively affected their predators, including walleye (*Sander vitreus*), northern pike (*Esox lucius*), and muskellunge (*Esox masquinongy*). A similar phenomenon has been reported in montane streams in the southern Appalachian Mountain region, where increases in stream temperature are limiting brook trout (*Salvelinus fontinalis*) habitat (McDonnell et al. 2015). Winter hypoxia in ice-covered lakes and resulting winter fish kills exclude large piscivorous fishes (Tonn and Magnuson 1982), but reductions in ice cover can change top-down controls, with cascading effects on lake communities, including small-bodied fishes, amphibians, zooplankton, and phytoplankton (Magnuson et al. 1985, Jackson et al. 2007). Increased lake temperature and low dissolved oxygen also favor nonnative species whose higher tolerance for variability enables them to outcompete native species (Rahel and Olden 2008). In summary, climate change can induce a cascade of ecological impacts on forest and freshwater ecosystems that alter species' abundance and composition across trophic levels, and may ultimately produce novel species assemblages.

Conclusions

This assessment of 40 years of research at nine forest and freshwater LTER sites indicates that long-term studies provide process-level information needed to comprehensively evaluate and understand how forest and freshwater ecosystems respond to climate change. Forest and freshwater LTER sites have experienced differential rates of climate change, varied environmental forcing, and diverse ecosystem responses. Although forests have demonstrated a remarkable ability to recover from extreme weather events, such as hurricanes and ice storms, forest and freshwater ecosystem responses to changing disturbance regimes continue to emerge. Continued monitoring of the long-term legacy effects of these disturbances will help in assessing climate change impacts on forest and freshwater ecosystems and the services they provide.

Despite many changes in ecosystems due to climate change, there is limited evidence of lasting shifts in ecosystem state at forest and freshwater LTER sites. The transition from boreal forest to deciduous forest species at Bonanza Creek in Alaska is the most prominent example; however, the long-term persistence of these deciduous stands is unknown given the uncertainty of future fire behavior and the successive recruitment dynamics of both hardwoods and conifers (Mack et al. 2021). In the tropical rainforest at Luquillo, despite high relative increases in extreme temperature and an increase in the frequency of hurricane disturbance and drought, there is little indication of ecosystem state change, or evidence of other abrupt ecosystem change, such as catastrophic declines in insect populations (Zimmerman et al. 2021). Nevertheless, it is possible that ecosystem state changes will occur in the future, highlighting the need for continued long-term research on climate change impacts and the resilience of forest and freshwater ecosystems.

Forest and freshwater ecosystems provide a wide range of beneficial goods and services (MEA 2005) that may be affected by climate change. Climate change is for the most part lessening supporting, regulating, provisioning, and cultural ecosystem services (figure 1). Examples include the loss of supporting services, such as habitat for fish in lakes (e.g., North Temperate Lakes; Magee et al. 2019); the loss of regulating services, such as flood protection in forests subjected to increased precipitation (e.g., Hubbard Brook; Campbell et al. 2011); the loss of provisioning services such as timber supply and quality due to wildfires (e.g., Andrews; Halofsky et al. 2020); and the loss of cultural services, such as subsistence opportunities for rural indigenous communities (e.g., Bonanza Creek; Kofinas et al. 2010). These changes in ecosystem services provide a strong basis for LTER research communities to continue engagement with policymakers and land managers to promote actions that address climate change (e.g., Driscoll et al. 2012, Swanson et al. 2021).

Long-term ecological research provides insights into climate change effects on forest and freshwater ecosystems that are not obtainable from short-term studies. The broad array of research emphases and approaches is a strength of the LTER Network and allows for in-depth, site-based analyses

of ecosystem responses. Continuing efforts to synthesize LTER data will facilitate future comparisons and improve our ability to test hypotheses across sites. Climate change effects on ecosystem services also should motivate continuing efforts for environmental stewardship. Forest and freshwater ecosystems are experiencing unique combinations of climate changes, environmental forcing, and compounding disturbances and stressors, and research investigating forest adaptation strategies and approaches to enhance resilience to climate change will help ensure that these ecosystems continue to deliver valuable services to society.

Acknowledgments

We gratefully acknowledge funding from the National Science Foundation's Long Term Ecological Research program that supports research at the Baltimore (through grant no. DEB-1855277), Bonanza Creek (grant no. DEB-1636476), Coweeta (grant no. DEB-1637522), H. J. Andrews (grants no. DEB-1440409 and no. DEB-2025755), Harvard Forest (grant no. DEB-1832210), Hubbard Brook (grant no. DEB-1637685), Luquillo (grant no. DEB-1831952), Niwot Ridge (grant no. DEB-1637686) and North Temperate Lakes (grants no. DEB-2025982 and no. DEB-1440297) sites.

Supplemental material

Supplemental data are available at *BIOSCI* online.

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